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## **Sexual Size Differences in Reptiles**

By

**Henry S. Fitch**

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MISCELLANEOUS PUBLICATION No. 70

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Sexual Size Differences in Reptiles

BY

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## INTRODUCTION

The kinds of vertebrates that have males and females of just the same average size are a minority. More often one sex or the other is larger. There are varying degrees of size difference, with a relatively large number of kinds having only slight sexual differences and relatively few kinds having major differences between the sexes. The present study was undertaken to clarify these relationships in reptiles.

Sexual size differences are better known in other groups of vertebrates than in reptiles. In fishes and amphibians females are usually larger than males, but there are noteworthy exceptions. In both birds and mammals males are usually larger than females. In birds the most outstanding exceptions are the raptors, both Falconiformes and Strigiformes, in which females are larger in varying degrees (Hill, 1944; Amadon, 1959). However, those raptorial birds that are mainly carrion-eaters or insectivores tend to have similar sized sexes, and the size difference is greatest in those kinds that take relatively large prey. In these predators the female takes larger kinds of prey, on the average and as a result the pair jointly occupying a territory, utilizes a wider range of prey which facilitates the securing of sufficient food, particularly during the critical period when nestlings are being fed. In accipitrine hawks Reynolds (1972) showed that the small male provides prey for the female during incubation and for the nestlings during the early stages of their growth, allowing the female to spend her time at the nest, protecting the brood against extremes of weather and predators; in the late stages of nestling growth, when the nestlings' need for food is maximal, the female is active in hunting, and provides relatively large prey items.

In mammals 84 species of 12 orders and about 30 families are known to have females larger than males (Ralls, 1976).

Mammalian groups that consistently have females larger include vespertilionid bats, rabbits (leporids), three families of baleen whales, lobodontine seals, and cephalophine and neotragine antelopes. These diverse groups seem to have no common traits such as polyandry, strongly developed female aggression, development of female weapons, or female dominance or matriarchy, that would account for the larger size of females.

Presumably the mean adult size of each species and the size relationships of its sexes are the products of a complex of selective pressures that change through time. Optimum adjustment to available food, shelter, and other environmental factors is involved. Some selective factors that might cause one sex or both sexes to deviate from modal adult size are: 1) need for the male to dominate potential mates and/or rivals; 2) need for the female to alter her reproductive strategy; 3) need for the species to reduce intraspecific (intersexual) competition for food and perhaps for other resources. Each species, in its unique ecological niche, has presumably been influenced by its own peculiar set of selective pressures.

The present study is a preliminary attempt to show general trends of sexual size differences in living species of the class Reptilia, and to determine causes and correlations for them. Most previous studies (e.g., Klauber, 1943; Shine, 1978b) have not undertaken to show the amount of sexual size difference, but have merely stated that one sex or the other was the larger. No survey for the group as a whole has been made heretofore, but a number of authors have indicated sexual size differences in individual species. In the iguanid lizard genera *Anolis* and *Sceloporus* I determined sexual size differences for a large number of species (Fitch, 1976, 1978) and indicated various ecological factors

that affected them; Schoener (1970) and Schoener and Schoener (1971a, 1971b) likewise determined sexual size relationships in many species of Antillean *Anolis*. However, my present study is a preliminary one because all figures obtained are in need of revision and/or refinement. Some data are based on inadequately small samples. Literature records are sometimes based upon different kinds of data, hence widely disparate figures have been obtained for the same kind of animal in a few instances. As data have accumulated, it has become evident that the sexual size difference of a species is subject to variation in time and space, and perhaps cannot be represented adequately by a single figure.

#### ACKNOWLEDGMENTS

The data that are the basis for this report were accumulated in the course of field work and museum studies over a 30-year period. W. Frank Blair (University of Texas, Texas Natural History Collection), Charles M. Bogert (American Museum of Natural History), W. E. Duellman (University of Kansas, Museum of Natural History), and Robert C. Stebbins (University of California, Museum of Vertebrate Zoology) kindly permitted examination of specimens in the collections under their care. Many persons assisted me in capturing the animals measured alive in the field, and in other ways; special thanks are due to Anthony A. Echelle, Alice Fitch Echelle, Chester W. Fitch, David C. Fitch, Virginia R. Fitch, Robert R. Fleet and Robert W. Henderson. My wife, Virginia R. Fitch, also helped me in various stages of gathering and analyzing the data and preparing the manuscript. Richard Shine shared with me the early planning of the study. Richard A. Seigel kindly contributed unpublished data concerning sizes in *Malaclemys*, Lawrence E. Hunt likewise contributed measurements for two kinds of *Anniella*. The following authors generously made available material from their unpublished manuscripts: Hugo

Hidalgo, Tsutomu Hikida, John B. Iverson, D. R. Jackson and R. Franz, Michael V. Plummer and D. B. Farrar. Alan E. Leviton kindly advised me concerning the correct names of various Asiatic species. W. E. Duellman kindly made available his measurements of Ecuadorian snakes and lizards, including substantial series of many species from Santa Cecilia and other localities in the Amazon Basin. These are indicated in Appendix I by the abbreviation "WED ms."

#### METHODS AND MATERIALS

Data pertaining to sexual size differences were collected during the course of field studies of several dozen local populations, in Kansas, Mexico and Costa Rica, and by examining museum specimens in the University of Kansas Museum of Natural History, the University of California Museum of Vertebrate Zoology, the American Museum of Natural History and the University of Texas Natural History Museum. Also, figures for many species were obtained from published literature. Most publications contained pertinent information on only one or a few species but some had relatively large amounts of information. Much information about African snakes was obtained from Laurent (1956, mostly maxima), FitzSimons (1962, maxima only), and Pitman (1974, maxima only). Likewise M. Smith (1943) presented much information about Indian snakes (maxima only) as did Wright and Wright (1957) for North American species (maxima and minima). Useful papers on entire herpetofaunas were those of Fuhn and Vancea (1961) for Romania (means), Dixon and Soini (1975 and 1977) for Amazonian Perú (maxima and minima), Duellman (1978) for Amazonian Ecuador and Hoogmoed (1973) for Surinam (means for some). Two exceptionally useful papers were those of Kopstein (1941) on Malayan snakes and Schwaner (1980) on Samoan skinks and geckos, both providing large series of individual

measurements for many species. Ernst and Barbour (1972) provided the source of much information on turtles. Information on specific groups of reptiles was obtained from the works of Blanchard (1921) on king snakes (with individual measurements), Dixon and Huey (1970) on South American geckos of the genus *Phyllodactylus* (means), and Klauber (1937) on rattlesnakes (means) and especially Schoener (1970) and Schoener and Schoener (1971a and 1971b) on West Indian anoles (means).

Male and female size was compared in the species studied by averaging all the adult measurements available for each sex. For snakes, lizards and crocodilians the measurements used were those of snout-to-vent (S-V) in nearly all instances, but a few figures from the literature were based on total lengths including tail. Tails are relatively longer in male reptiles than in females, so inclusion of the tail measurement would increase the apparent sexual size difference in kinds having relatively large males but would reduce or nullify it in kinds having relatively large females. Many authors indicated total lengths for individual specimens, and the ratio of tail length to total length. In such instances I calculated snout-vent length for each specimen by subtracting tail length, assuming its tail ratio was the same as the mean for the series, but doubtless with loss of precision. Some authors showed the lengths S-V of individuals or classes in histograms without presenting actual figures; I undertook to convert data from these graphs to the original figures. In turtles the length measurements used were those of the carapace for most species and those of the plastron for some others.

Females of different reptile species investigated ranged from about  $\frac{1}{2}$  to  $2\frac{1}{2}$  times mean male length. Since bulk increases as the cube of linear dimensions, it is implied that females weighed from about one-fourth to about 15 times as much as their male counterparts.

Differences between the sexes in specific gravity and in bodily proportions, which might affect the accuracy of relative weight calculations based on linear measurements, are probably of minor significance in most instances. Relatively few authors have recorded actual weights for reptiles, but such data are highly desirable.

Determining the lower limits of adult size was critical. In females, pregnancy or production of yolked follicles was considered adequate proof of sexual maturity. Likewise in males production of sperm was a valid criterion. However, in practice it was often not possible to check live animals or museum specimens for eggs or sperm. Instead, the development of various secondary sexual characters were relied upon. Also, the maximum size for each sex and the size distribution of a series were taken into account in deciding upon the minimum size to be included as adults. Inasmuch as small (younger) adults were usually much more numerous than large (older) adults whose cohorts had been reduced by normal mortality factors, the curve for each series tended to be skewed, with mean nearer the lower end. Even a small change in the minimum size included might have had important effect on the mean.

The following abbreviations have been used:

SSD = sexual size difference

FMR = female-to-male ratio

The latter was the linear measurement of snout-vent length, or shell length always expressed as a per cent; for example male S-V = 350 mm, female S-V = 400 mm, FMR =  $400/350 = 114$ ; or, as a second example, male S-V = 400 mm, female S-V = 360 mm, FMR =  $360/400 = 90$ . The figure for FMR has in all instances been rounded to the nearest whole number.

Under Results such figures, based on averages for series of adult males and females, are presented for many species.

These figures, obtained from a variety of sources, mostly from published literature, represent four degrees of reliability. The most reliable are those figures based on the means of large statistical series (sometimes several hundred). Such records are distinguished in the lists by having both the name of the species and the figure representing its FMR set in bold face. Less reliable are figures based on means from fewer than ten measurements for either sex. These are distinguished by the symbol  $\bar{x}$  following the FMR figure. Thirdly, there are figures based on the FMR for the modes, when the author had indicated only the maximum and minimum measurements for adults of each sex. For example: male S-V = 250 to 350 mm (mode 300), female = 300-400 (mode 350), FMR = 350/300 = 117. Such records are designated by the letter "m" following the FMR figure. Even less reliable are ratios obtained from maximum measurements for each sex. Such figures are included only where it is believed that the author measured a substantial series of each sex, but often the number of specimens was not mentioned. Eliminating all such instances would have assured more consistent trends, but also would have eliminated many important groups for which no information was available otherwise. In order to avoid a spurious impression of accuracy, the actual FMR figures obtained from maximum measurements have not been presented, but instead a code has been substituted, as follows:

FMR > 135: +++++  
FMR 126-135: ++++  
FMR 116-125: +++  
FMR 106-115: ++  
FMR 96-105: +  
FMR 86-95: X  
FMR 76-85: --  
FMR 66-75: ---  
FMR < 66: ----

The 548 taxa for which only maximum measurements for each sex are available are listed in Appendix II. In general

these figures are considered to be useful at least for showing which sex is the larger, and whether SSD is large or small. They show significant trends in groups for which, otherwise, little information is available. For instance in the Asiatic *Trimeresurus*, 13 species were shown to have females larger, three species had the sexes about equal and only one was shown to have the male larger, in records mostly obtained from Smith (1943).

Most samples that were used consist of statistical series of each sex reported in the literature, and usually the series represent a single locality or area. In a few instances it was necessary to combine measurements published by two or more authors; for several species of African snakes, means were obtained by combining figures of several authors including Broadley and Cock (1975), Fitz-Simons (1962), Laurent (1956), Loveridge (1953), Pienaar (1966), Pitman (1974), Schmidt (1923) and de Witte (1953), in various combinations. Each of these authors published the maximum figures for the series available to him, and the means for these maxima are, of course, relatively high, compared with means from randomly selected series that are available for most other species. Likewise for several Asiatic snakes, averages were obtained from maximum measurements published by Pope (1935), Smith (1943), Malnate (1962), and others.

In general, however, the figures in Appendix I are believed to be representative for each of the species in showing the approximate mean sizes of adults of both sexes and the usual range. Appendix I will no doubt have some usefulness in showing typical sizes for various species, since definitive statements about size are remarkably scanty in the literature. Even revisionary studies which treat lepidosis and body proportions in great detail usually contain no useful information concerning size. Often the only statement about size is that of the total length of the largest specimen

examined (sometimes with no indication of its sex). Herpetologists have been prevented from fully utilizing size in systematic studies by the dogmatic conviction that in reptiles growth is "indeterminate." Actually the genetic size differences between species and subspecies could, in my opinion, provide some of the most useful taxonomic characters. In general, adult size in a reptile species is more variable than it is in a bird or mammal, but less so than in a fish. Adult size tends to be relatively homogeneous in turtles and lizards, less so in snakes; but within each of these groups there is much difference between families, genera and species in homogeneity of adult size.

In the annotated systematic listing, under *Results*, binomials are used (regardless of subspecies) when only one population of a species was sampled, or for the nominate subspecies if other populations of the species are listed separately.

The maximum sizes listed in the appendices include few "world records" if any. They merely represent the largest male and female in the particular series utilized, and almost inevitably larger specimens will be found if they are not already known.

Although most FMR figures were obtained from random samples of adults, there were several important exceptions. The figures for many West Indian anoles, from Schoener (1970) and Schoener and Schoener (1971a and 1971b) were based on the one-third of the adults of each sex that were the largest in each sample. The figures for Conant's (1969) Mexican *Nerodia* were based on the 10 largest males and females of each sample. In a few instances, disregarding trinomials and minor geographic variants, I averaged the maxima for several geographical populations to obtain a series (e.g., Schwartz, 1970). In a few instances as for the several African snakes the maximum measurements for each sex pub-

lished by various authors were combined to average for FMR.

A series of specimens showing a sexual size difference usually has more difference between the maxima than between the means, that is, the difference between the male and female means tends to be magnified in the maxima. The trend of relationship between means and maxima are shown in Table 1. Even if the means are just the same, one sex or the other may grow to a larger maximum size.

## RESULTS

The large amount of data obtained bearing on sexual size differences in reptiles has revealed some significant trends within and between various taxonomic groups. Also it has raised many problems that are not readily answered. For most reptile species knowledge of life history and ecology is still insufficient to interpret SSDs in terms of reproductive strategies, *r* and *K* selection or other appropriate concepts.

Ontogenetic changes in sexual size differences are revealed for several species. For several others, geographic variation in SSD is shown. In some cases SSD can be strongly correlated with behavioral or reproductive traits or with climatic preferences.

Table 1 shows FMR figures for 30 species of turtles, lizards and snakes for which large series of adults were available. It compares various other parameters with the FMR means, showing that in most instances the mode, median, and means for the 10 largest of each sex (or 5 largest, or 3 largest) approximate the series mean, but the ratio of maximum male and female measurements is more variable. Except where otherwise indicated, by asterisk, the species in Table 1 are those measured by me in field studies of live animals or in studies of museum specimens.

Excluding those 548 taxa for which only maximum measurements for each sex were available, 770 kinds of reptiles

were checked for size difference between the sexes. Twenty-five had males and females of approximately the same size, 371 had females averaging larger than males, and 374 had males averaging larger than females. For the whole group average female size was 104% of male size (66%-248%).

### ONTOGENETIC CHANGE

Sexual size differences are discussed throughout most of this paper as if they were constant and species-specific. Ontogenetic changes have been shown for

a few kinds, but figures are less refined than could be desired. Although some studies were based on large-scale marking of individuals, the survivors in the older age groups were generally so few that their means were subject to fairly wide margins of error.

The usual trend seems to be growth at comparable rates in juveniles of both sexes, with divergence in size at adolescence, and little change in SSD during the period of slowing growth after average adult size is attained. Table 2 shows male and female sizes (S-V) in successive

TABLE 1. FMR (= ratio of female length to male length expressed as per cent).

Species	N	N	$\bar{x}$ (FMR)	mode	median	maximum	10 largest	5 largest	3 largest
<i>Turtles</i>									
<i>Gopherus agassizii</i> *	59	32	92	89	79	95	90	92	92
<i>Pseudemys scripta</i> *	98	48	140	146	125	103	109	107	106
<i>Terrapene ornata</i>	78	163	101	100	102	103	103	103	104
<i>Lizards</i>									
<i>Ameiva undulata</i>	44	69	85	84	85	92	88	91	92
<i>Cnemidophorus deppei</i>	152	260	93	87	88	88	88	88	88
<i>Cnemidophorus sexlineatus</i>	88	96	101	101	100	102	102	103	102
<i>Cnemidophorus tigris</i>	46	75	93	95	96	89	93	90	89
<i>Eumeces fasciatus</i>	120	180	99	100	100	96	98	98	98
<i>Eumeces obsoletus</i>	146	128	102	102	104	106	104	104	105
<i>Ophisaurus attenuatus</i>	733	420	95	95	96	92	92	92	91
<i>Sphenomorphus cherriei</i>	39	61	100	102	101	109	103	106	109
<i>Snakes</i>									
<i>Agkistrodon contortrix</i>	116	98	93	94	95	76	85	80	77
<i>Bothrops atrox</i>	59	53	115	111	116	116	122	122	119
<i>Carpophis vermis</i>	90	73	117	116	114	113	119	116	114
<i>Coluber constrictor</i>	181	177	110	109	107	109	117	117	116
<i>Diadophis punctatus</i>	906	408	111	114	117	126	119	123	123
<i>Dipsas catesbyi</i>	99	105	96	101	101	109	126	105	108
<i>Elaphe obsoleta</i>	255	168	98	94	103	87	88	89	89
<i>Lampropeltis calligaster</i>	78	75	91	93	91	90	88	89	90
<i>Lampropeltis triangulum</i>	47	35	97	99	97	85	93	92	91
<i>Leptodeira annulata</i>	45	51	108	103	107	110	108	108	109
<i>Liophis miliaris</i> *	123	244	124	123	130	134	141	139	139
<i>Micruurus fulvius</i> *	46	92	119	122	116	158	142	144	158
<i>Nerodia sipedon</i>	55	46	132	134	134	137	138	137	134
<i>Pituophis melanoleucus</i>	59	55	101	104	104	91	100	99	96
<i>Sonora episcopa</i> *	347	302	100	100	100	100	100	100	100
<i>Thamnophis ordinoides</i>	21	28	123	124	124	130	128	128	128
<i>Thamnophis sirtalis</i>	215	282	123	125	160	182	177	180	180
<i>Tropidoclonion lineatum</i> *	137	175	117	115	132	131	130	124	129
<i>Virginia striatula</i> *	90	55	116	119	123	119	123	127	117

\* Clark, 1964, for *Virginia striatula*; Force, 1936, for *Tropidoclonion lineatum*; Gans, 1964, for *Liophis miliaris*; Kassing, 1961, for *Sonora episcopa*; Moll and Legler, 1971, for *Pseudemys scripta*; Quinn, 1979, for *Micruurus fulvius*; Woodbury and Hardy, 1948, for *Gopherus agassizii*.

annual age classes of seven reptile species including one lizard and six kinds of snakes.

In the account of *Alligator mississippiensis* based on a large scale field study by Chabreck and Joananen (1979), it is shown that juvenile males grow faster than females, and although there is some slowing of growth at adolescence, adult males continue to grow faster than adult females. Hence, in the oldest alligators SSD is extreme.

Ernst (1977) presented figures on the sizes of adult *Clemmys muhlenbergii* of different ages that seemed to indicate little change in the size ratio of the sexes as the turtles grew older. In series that were 6, 7, 8, 9, 10 and 11 years of age the female-to-male size ratios were, respectively, 93, 92, 93, 93, 94 and 93 per cent. Both sexes increased in size by 31% from the 6- to 11-year-old class. There were 10 to 17 turtles of each sex in each year class, except 11-year-olds with 4 males and 7 females.

In the large Neotropical iguanid, *Basiliscus basiliscus*, both sexes grow at approximately the same rate for nearly a year, to about 2.5 times hatchling size of 42 mm (S-V). Thereafter, approaching adolescence, the females grow more slowly than males. In the oldest basilisks (6+ years) female to male ratio has decreased to about 72% ( $\delta$  229 mm,  $\varphi$  165) but SSD is less in some localities (Van Devender, 1978).

#### GEOGRAPHIC VARIATION

Polytypic species have shown geographic change in the size ratio of the sexes in every case tested, and it may be speculated that such change is the rule. Several examples are presented in Tables 3 to 5. *Uta stansburiana*, being abundant and widespread, provides one of the best examples, and the data for 19 local populations are compared in Table 3. The first 10 populations are from the western United States and Mexico from  $45^{\circ}$  N in Oregon to  $28^{\circ}20'$  N in west-central Sonora, and FMRs range

from 87.5 to 100.1. There is not a clear-cut latitudinal gradient, but in all six of the more northern populations (north of latitude  $35^{\circ}$ ) FMR exceeds 93 ( $\bar{x} = 95.7$ ) whereas in the four more southern populations FMR is consistently less than 93 ( $\bar{x} = 90.0$ ). Nussbaum and Diller (1976), who studied the northernmost population in north-central Oregon, found that male aggression was little developed, compared with that of more southern populations. The nine populations represented in the lower half of Table 3 are from various islands in the Gulf of California. Their sexual size dimorphism is comparable to that of mainland populations. Both in having males relatively large in insular populations and in having males relatively larger in southern than in northern populations, *Uta stansburiana* follows trends that are widespread in lizards.

*Cnemidophorus tigris* is another wide-ranging, polytypic lizard species and samples from the northern and southwestern parts of the range showed the sexes to be approximately equal in size with males averaging slightly larger. However, in samples from the southeastern part of the range, south-central New Mexico (Medica, 1967) and Reeves County, Texas (Fitch, 1970) males averaged markedly larger than females (FMRs 87 and 94).

Table 5 shows sexual size differences in geographic populations of *Chrysemys picta*. This wide-ranging species is typical of many freshwater turtles in having females much larger than males, the latter maturing at relatively small size and early age. In this table, for each population, the length (plastral) shown is the minimum at sexual maturity, rather than the adult average, as in most other instances. Although no well defined gradient is discernible, there seems to be a general trend toward having relatively much larger females in the southern half of the United States than in the northern half. Extreme size differences in the sexes results from early sexual

TABLE 2. Ontogenetic Changes in Sexual Size Ratios in Lizards and Snakes: Male and Female Lengths (S-V in Millimeters) and FMRs.

Species	Year of Life						Authority			
	Second	Third	Fourth	Fifth	Sixth	Seventh				
<i>Aegista</i> <i>trodon</i> <i>contortrix</i>	474* 468	99	564 537*	95 591	637 591	94 609	702 620	— — Fitch, 1960		
<i>Amphibolurus</i> <i>maculatus</i>	64* 59*	92.3	67 61	91 62	70 62	88.5 —	— —	Mitchell, 1973		
<i>Coluber</i> <i>constrictor</i>	615* 644*	105	706 810	114 866	757 115	810 923	827 965	— — Fitch, 1963		
<i>Diadophis</i> <i>punctatus</i>	180* 191	106	224 240*	107 264	240 110	249 277	256 284	261 290	111 111 266 298	112 — Fitch, 1975
<i>Elaphe</i> <i>quadrivirgata</i>	796 703	92	1038* 954*	92 1040	1235 83.2	1425 1140	80.2 —	— —	— — Fukada, 1965	
<i>Rhaldophis</i> <i>tigrina</i>	678* 731*	108	765 878	114.9 1010	840 120	— —	— —	— —	— — Fukada, 1964	
<i>Thamnophis</i> <i>sirtalis</i>	455* 550*	121	515 625	121 690	550 735	585 126	615 775	126 — — —	— — Fitch, 1965	

\* Sexual maturity

maturity in males—at a minimum age of only two years whereas females require at least four years. In more northern regions male maturity is delayed until somewhat larger size is attained, at four or five years, and female maturity requires six to ten years.

Iverson (ms) studied SSD in the Mexican mud turtle, *Kinosternum hirtipes*. In a sample of 306 adult males and 237 adult females FMR was 92.3. However, the species has many discrete populations isolated from each other in separate drainage basins and differing in various

TABLE 3. Geographic Variation in Sexual Size Ratios in *Uta stansburiana*.

FMR (Female to male length ratio per cent)	S-V ♂ N	S-V ♀ N	Geographic origin	Authority
93.9	48.4	45.4	North Central Ore.	Nussbaum and Diller, 1976
95.0	47.55 ( 47)	45.04 ( 25)	Hart Mtn. Antelope Refuge, Ore., 42°25'	Parker & Pianka, 1975
100.1	48.56 (107)	48.72 (104)	3-4 km W Grantville, Utah, 40°36'	Parker & Pianka, 1975
96.5	48.26 ( 27)	46.53 ( 36)	8 km N Lovelock, Nev. 40°12'	Parker & Pianka, 1975
93.5	48.22 ( 18)	45.15 ( 26)	Kyle Canyon, Nev. 36°15'	Parker & Pianka, 1975
95.6	51.85 ( 55)	49.56 ( 69)	8 km N Mojave, Calif. 35°06'	Parker & Pianka, 1975
91.5	51.71 (102)	47.38 (114)	S Mtn, Phoenix, Ariz. 33°26'	Parker & Pianka, 1975
92.4	55.34 (101)	51.11 ( 91)	16 km NW Casa Grande, Ariz. 32°57'	Parker & Pianka, 1975
88.6	50.39 ( 18)	47.44 ( 16)	Dona Ana and Luna Cos, NM 31°50'	Parker & Pianka, 1975
87.5	53.29 ( 17)	47.05 ( 21)	7 km E Estero de Tastiota, Sonora 28°20'	Parker & Pianka, 1975
94.0	44.59 ( 32)	41.83 ( 24)	Isla San Francisco	Dunham & Tinkle, 1978
91.0	50.88 ( 16)	46.28 ( 25)	Isla San José	Dunham & Tinkle, 1978
88.6	45.95 ( 20)	40.67 ( 18)	Isla Partida Sur	Dunham & Tinkle, 1978
91.1	44.88 ( 17)	40.89 ( 18)	Isla San Marcos	Dunham & Tinkle, 1978
91.1	51.50 ( 34)	46.85 ( 34)	Isla Carmen	Dunham & Tinkle, 1978
93.1	49.56 ( 25)	46.04 ( 26)	Isla Tortuga	Dunham & Tinkle, 1978
91.5	48.50 ( 18)	44.39 ( 26)	Isla Tiburon	Dunham & Tinkle, 1978
92.2	52.48 ( 27)	48.36 ( 47)	Isla Partida Norte	Dunham & Tinkle, 1978
94.4	47.21 ( 39)	44.60 ( 30)	Isla San Esteban	Dunham & Tinkle, 1978

TABLE 4. Geographic Variation in Sexual Size Ratios in *Cnemidophorus tigris*.

FMR ♀ to ♂ ratio, percentage S-V	♂ S-V range N	♀ S-V range N	Region	Authority
99.8	94.8 (93-97 in 10)	94.6(91-102 in 10)	SW Idaho	Burkholder & Walker, 1973
99.4	77.6 (97-66 in 22)	77.1(88- 69 in 9)	L. Colorado River	Vitt & Ohmart, 1977b
97.7	85.6 (79-95 in 52)	83.7(71- 98 in 43)	Test Site, S Nevada	Tanner & Banta, 1966
93.6	83.5 (79-95 in 44)	78.1(71- 87 in 79)	Reeves Co., Texas	Fitch, 1970
87.1	82.24(64-97)	71.6(54- 88)	S-Central New Mex.	Medica, 1967

TABLE 5. Relative Lengths of Males and Females of *Chrysemys picta* at Sexual Maturity.

FMR	Male at sexual maturity		Female at sexual maturity		Region (state in USA)	Authority
	length	age (yrs.)	length	age (yrs.)		
175	70		120-125		S. Ill.	Cagle, 1954
175	60-65	2-3	100	4	La., Ark.	Moll, 1973
162	65	2-3	105	4-5	Tenn.	Moll, 1973
158	80-85	3-4	130	4-6	Cent. Ill.	Moll, 1973
153	80-90		130		New Mex.	Christiansen and Moll, 1973
147	85+		125+		S. Minn.	Legler, 1954
144	80	5	110-120	7-10	S. Mich.	Gibbons, 1968
141	95-100	4-5	135-140	7-8	Wisc.	Christiansen and Moll, 1973
139	90		120-130		N. Mich.	Cagle, 1954
118	80-90	4	100	4-6	Penn.	Ernst, 1971
117	95-100	4-5	135-140	7-8	S. Mich.	Wilbur, 1975

characters including SSD. Drainage basins in Mexico that yielded substantial series, and the FMRs obtained from them were as follows: Papigochic 85.9 (22 males, 23 females), Conchos 86.5 (56 males, 42 females), Nazas 92.0 (20 males, 13 females), Santa Maria 92.3 (39 males, 25 females), Aguanaval 95.8 (28 males, 22 females), Mezquital 100.2 (28 males, 29 females). Seven other populations represented by only small samples had FMRs exceeding 100. Iverson found a trend for the smaller drainages and those containing lakes to have populations of relatively small turtles in which there was little size dimorphism or else female-favored size dimorphism.

In the Neotropical lizard, *Anolis cupreus*, massive samples are available to show geographic variation in sexual size differences over the range. The males are markedly larger. In *A. c. cupreus* and *A. c. spilomelas* of the lowlands of northwestern Costa Rica, FMRs are 88 and 84, respectively, and 82 in *macrophallus* of Guatemala. But in *A. c. hoffmanni* at the upper altitudinal limit, on the Meseta Central of Costa Rica, FMR is 97. The intraspecific trend in *A. cupreus* conforms with interspecific trends in the large genus *Anolis*. Those kinds in severely seasonal climates where cold or drought prevent reproduction over part of the year, with a rela-

tively concentrated and stressful breeding season, have relatively larger males than do kinds living in climates that tend to be aseasonal, such as rain forests and montane cloud forests.

*Ameiva auberi* is a small terrestrial teiid lizard that is widely distributed over the West Indies, with named subspecies on many islands. There is much intraspecific variation in size and also, apparently, in size ratios of the sexes, but figures are available only for maximum sizes of each sex (Schwartz, 1970; McCoy, 1970). Excluding small samples (those in which less than 28 specimens were available) there were 15 population samples from Cuba and neighboring islands, and 7 samples from the Bahamas, with from 28 to 123 specimens. FMRs ranged from 95.7 (*auberi*, N coast of Cuba) to 59.6 (*multilineata*, Berry Islands, Bahamas). For the entire group of 22 populations, FMR averaged 79.3, but it averaged much lower (70.3) for the 7 Bahamian subspecies than for the 15 from Cuba and vicinity (82.6). Despite this regional difference, the subspecies showed no obvious correlation with size of island, body size, or any other obvious factor in the trend of their sexual size difference.

In West Indian anoles presence or absence of congeneric competitors seems to be a major factor affecting SSD.

Schoener (1970) and Schoener and Schoener (1971a, 1971b) have published figures for many populations, in sympatry and allopatry, showing varying degrees of character displacement. For each species I arbitrarily selected one FMR figure when several were available, to include in Appendix I and the annotated list. SSD in anoles is further discussed below in the annotated list.

### ANNOTATED SYSTEMATIC LIST

In the following list the various groups of reptiles are treated in the usual systematic sequence. Under each major group, genera and species are listed alphabetically, with a figure or symbol indicating FMR of each species, followed by brief comments on the trends within the group, and possible explanations for them. The groups first tested were families but some were combined into larger systematic units or divided. Data were obtained for relatively few kinds of turtles, hence there is only one list for the order Testudines, but there are many lists for the order Squamata and its main subdivisions, the snakes and lizards. In the large ophidian family, Colubridae, 24 subfamily units are separately listed, because substantial series of species were available in some, with distinctive trends setting them off from other subfamilies. Similarly, the large family Iguanidae is divided into seven subfamily units to treat with the 226 taxa for which definite FMR figures are available. I follow Etheridge (1964, 1965, 1966) in the iguanid subfamilies recognized, except that I have also included "crotaphytines" and "phrynosomines" not formally designated by Etheridge but implied by him in dissociating *Crotaphytus* and *Phrynosoma* from the sceloporine genera. Both are sufficiently distinctive in the trends of their SSD to merit separate treatment.

### Testudines

*Chelonia mydas* 106 m, *Chelydra ser-*

*pentina* 100 ♂, *Chersina angulata* ---, *Chrysemys picta* 139, *Clemmys guttata* 100, *C. marmorata* 100 m, *C. muhlenbergii* 107, *Deirochelys reticularia* 194 m, *Emydoidea blandingii* 95, *Emys orbicularis* 106 m, *Eretmochelys imbricata* 104 m, *Geochelone elephantopus ephippium* 82, *G. e. vicina* 99, *G. pardalis* +++, *G. p. babcocki* +, *G. radiata* 93 ♂, *Gopherus agassizii* 92, *G. polyphemus* 106 m, *Graptemys barbouri* 195 m, *G. geographica* 196, *G. kohni* 182 m, *G. nigrinoda* 143 m, *G. oculifera* 184 m, *G. ouachitensis* 167, *G. pseudogeographica* 169, *G. pulchra* 248 m, *Homopus areolatus* ++, *H. boulegeri* X, *H. femoralis* ++, *Kinixys belliana* +, *K. b. nogueyi* X, *K. erosa* ---, *K. homeana* X, *Kinosternon bauri* 101 ♂, *K. b. palmarum* 121 m, *K. flavescens* 98, *K. subrubrum* 118 m, *K. s. hippocrepis* 100, *Lepidochelys olivacea* +, *Macrochelys lacertina* 86, *Malaclemys terrapin* 158 m, *M. t. centrata* 144 ♂, *M. t. tequesta* 141, *Malacochoerus tornieri* ++, *Psammobates oculifer* +, *P. tentorioides* +++, *P. t. verroxi* ++, *Pseudemys concinna* 117 m, *P. floridana* 139, *P. f. "suwanensis"* 143 m, *P. f. texana* +, *P. rubriventris* 116 ♂, *P. scripta* 140, *P. s. troosti* 108 m, *Rhinoclemys annulata* +, *R. areolata* +, *R. funerea* -, *R. nasuta* +, *R. pulcherrima* +, *R. p. incisa* 117 ♂, *R. p. manni* ++, *R. p. rogerbarbouri* +++, *R. punctularia* +, *R. p. diademata* +++, *R. rubida* ---, *R. r. periantha* +, *Sternotherus carinatus* 98, *S. minor* 105, *S. odoratus* 105, *Terrapene carolina* 91 ♂, *T. coahuila* 93, *T. ornata* 102, *Testudo graeca* 97 m, *T. kleinmanni* +, *Trionyx muticus* 158, *Trionyx spiniferus emoryi* 236 m, *T. s. ferox* 168, *T. s. pallidus* 182 m.

The FMR samples, representing 50 taxa (all cryptodiran) averaged  $129.8 \pm 5.68$ . Females were larger in 70%, males in 22% and sexes were equal-sized in 8%.

The most striking aspect of these figures is the relatively large size of females in most species, and especially in those of highly aquatic habits. In those kinds having the males larger, the

difference is usually small, and most such species have terrestrial tendencies. Although precise figures are not available for any pleurodiran, Roze (1964) wrote of the giant South American river turtle *Podocnemis expansa* that adult females averaged about two feet in shell diameter, males about 1½, hence FMR probably approximates 133. Relative large female size is most extreme in the emydid genus *Graptemys*. In *G. pulchra* of Alabama adult male size is 80-120 mm, whereas adult females are 212-285 mm (Shealy, 1976). Males mature in their third or fourth year, but females require about 14 years to mature. In soft-shelled turtles the SSD is almost as great. Plummer (1977) found FMR of 158 in *Trionyx muticus*. Associated with this great size difference there was striking difference in habits and behavior. Males spent more time in basking and tended to keep in shallow water in relatively small home ranges, but in contrast the large females spent their time in deep water in the main channel of the river, with relatively long movements upstream and downstream. Plummer and Farrar (ms) studied food habits of *T. muticus* from the stomach contents of 105 adults of this same population. The diet of males was found to be more diverse than that of females, and significantly different numerically and volumetrically. Approximately 71% of the food volume taken by females consisted of aquatic organisms, of which larvae of the trichopteran *Hydropsyche* were by far the most numerous, whereas approximately 67% of the food volume taken by males consisted of terrestrial items. The most important items for males, in order of decreasing volume, were: mulberries 34.3% (48), cottonwood seeds 15.3% (892), trichopteran larvae 10.4% (456), dipterans 6.3% (139), beetles 4.2% (206), fish 1.7%, lepidopterans 1.2% (9). In contrast, the most important items for females were: trichopteran larvae 43.7% (2430), fish 20.1%, mulberries 16.3% (28), crayfish 4.9% (7), beetles 2.3% (17) and ephemeropteran

larvae 1.9% (59). No significant relationship was evident between prey size and turtle size, nor between prey size and sex of turtle.

Males are larger than females in the tortoises *Geochelone* species and *Gopherus agassizii*, the box turtle *Terrapene carolina*, the emydids *Clemmys muhlenbergii* and *Emydoidea blandingii*, the chelydrids, *Chelydra serpentina* and *Macrochelys lacertina*, and the kinosternid, *Kinosternon flavescens*. In all of these and in many other kinds of turtles male aggression is known to occur. Harless (1978) summarized the literature on agonistic behavior in turtles. Eleven accounts pertained to *Terrapene* and 11 others to testudinids (*Chersine*, *Geochelone*, *Gopherus*); 8 were of chelydrids, 8 were of *Clemmys*, 5 were of kinosternids (*Kinosternon*, *Sternotherus*), 4 were of chelonids (*Chelonia*, *Eretmochelys*), 2 were of *Chrysemys*, 2 were of *Trionyx* and 1 was of *Graptemys*.

Male combat is prominent in some species in which the sexes are nearly the same size, or in which the female is a little larger. In *Chelonia mydas* Booth and Peters (1972) described attacks on the mating male by "attendant" males.

In captive turtle groups, including tortoises, box turtles, and *Clemmys insculpta*, males are known to form dominance hierarchies. Agonistic behavior consists of biting and ramming. Threatening posture, rapid approach, hissing, and odors including those of the feces, reinforce dominance. Dominant males may inhibit the feeding and mating activities of other males. Under natural conditions turtles are not known to have polygynous mating systems, and males rarely, if ever, maintain discrete territories.

It should be noted that much different FMRs have been obtained for the same species of turtles in a few instances when two or more authors have published different sets of figures. For instance, for *Chelydra serpentina* an FMR of approximately 100 is indicated both

from White and Murphy's (1973) plastral measurements and Christiansen and Burken's (1979) carapace measurements, whereas Mossman and Bider's (1960) carapace measurements of a Quebec population indicate FMR of 88. For *Kinosternum subrubrum* Mahmoud's (1967) figures indicate FMR of 100 whereas Iverson's (1979a) indicate FMR of 118. It needs to be determined how much such differences actually reflect geographic or ontogenetic variation vs. authors' biases in collecting, or in their criteria for setting the lower limits of adults of each sex.

### Squamata: Sauria

**GECKONIDAE.** *Aristelliger georgeensis* —, *A. hechti* —, *A. lar* —, *A. praesignis* —, *Coleodactylus amazonicus* 105, *Coleonyx brevis* X, *C. elegans* X, *C. mitratus* X, *C. variegatus* 107, *C. v. utahensis* 114, *Cosymbotus platurus* 99, *Cyrtodactylus malayanus* 109, *C. pubisculus* 110, *Eublepharus angramainyu* 89 ♂, *Garthia dorbignyi* X, *G. penai* X, *Gecko japonicus* —, *G. vittatus* X, *Gehyra australis* 104 ♂, *G. oceanica* 97, *G. variegata* 99 ♂, *Gonatodes albogularis* 100, *G. annularis* 101 ♂, *G. concinnatus* 99 ♂, *G. humeralis* 106 m, *Hemidactylus frenatus* 96, *H. mabouia* 106 m, *H. turcicus* 106, *Heteronotia binoei* 108, *Lepidodactylus lugubris* 102 ♂, *Lygodactylus angolensis* X, *L. capensis* X, *L. picturatus* —, *Pachydactylus punctatus* +, *P. tuberculatus* —, *Palmatogecko rangei* ++, *Peropos mutilatus* 99, *Phelsuma laticauda* —, *P. lineata* —, *P. madagascarensis* —, *Phyllodactylus angustidigitatis* 95, *P. europaeus* 98 ♂, *P. gerrhopygus* 98, *P. inaequalis* 100, *P. interandinus* 105, *P. johnwrighti* 103, *P. kofordi* 102, *P. lepidopygus* 115, *P. microphyllus* 100, *P. reissi* 97, *P. tuberculatus* 102 m, *P. ventralis* 100, *Pseudogonatodes guianensis* 102 ♂, *Ptenopus garrulus* 101 ♂, *Sphaerodactylus argivus* 99, *S. argus* 113, *S. a. bartschi* 106, *S. cinereus* X, *S. copei astreptus* X, *S. c. pelates* X, *S. c. websteri* X, *S. lewisi* 108, *S. oxyrhinus* 111, *S. o.*

*daenicolor* 102, *S. rosaura* X, *S. semasiops* 110, *Tarentola americana* —, *T. mauritanica* 84, *Thecadactylus rapicaudus* 106 ♂.

Among 43 species of geckos tested, FMR ranged from 84 to 115, and averaged 101.9. Males were larger in 13 species; females were larger in 26, and the sexes were equal in four. Eleven of these geckos were members of the large genus *Phyllodactylus* and in all but one of these males and females averaged nearly equal in size. The exception was *P. lepidopygus* having a FMR of 115. The remaining 32 species of geckos were in 15 genera representing Europe, Africa, Asia, Australia and South and Central America. The species having relatively largest males, *Tarentola mauritanica* (FMR 84) and *Eublepharis angramainyu* (FMR 89) are from the temperate-zone climate of Spain and Iran, whereas most of those with relatively large females were from equatorial regions.

Geckos are known to maintain territories, with visual cues and vocalizations playing important roles. Males are more aggressive, and in some instances there is dimorphism, with males more conspicuously marked. Large males would seem to have a selective advantage in defending territories and securing mates. Especially where there is a relatively short and concentrated, and therefore stressful breeding season, large size might confer selective advantage. Oviparity is the rule (except in New Zealand) with a two-egg clutch (or one egg, in sphaerodactylines and a few small geckonines). The hatchlings are relatively large. Large hatchlings probably have better chances of survival than small ones. Doubtless there is selective pressure for females to produce larger young, counteracted by selection for light weight, in these small scansorial lizards dependent on their digital lamellae to cling to surfaces that are sometimes smooth and vertical.

**IGUANIDAE.** This is a large and diverse family of lizards, mostly of the Western Hemisphere. They range from

small to large. They are vision-oriented, and there are usually special display organs in the males, less developed or lacking in the females. The displays are stereotyped and species-typical, and serve both in territorial aggression and defense and in courtship. Most iguanids are oviparous but several genera of basiliscines, sceloporines, phrynosomines and tropidurines have some viviparous species. Average clutch size ranges from just one in anolines to several dozen in large mainland iguanines.

**ANOLINAE.** *Anolis aeneus* 71, *A. ahli* —, *A. allisoni* 74, *A. allogus* 75, *A. alumina* —, *A. alutaceus* 92, *A. angusticeps* 88, *A. aquaticus* 89  $\bar{x}$ , *A. argillaceus* 81, *A. attenuatus* 95, *A. auratus* 104  $\bar{x}$ , *A. a. sipaliwinensis* 104, *A. baleatus* —, *A. b. litorisilva* —, *A. b. multistruppus* —, *A. b. scelestus* —, *A. bahorucoensis southerlandi* —, *A. barahonae* —, *A. barkeri* —, *A. bimaculatus* 71, *A. biporcatus* 102, *A. biscutiger* 106, *A. bombiceps* 110 m, *A. bourguae* 103, *A. bremeri* 70  $\bar{x}$ , *A. brevirostris* 89, *A. capito* 106, *A. carolinensis* 79, *A. carpenteri* 105  $\bar{x}$ , *A. chlorocyanus* 76, *A. christophei* 92, *A. chrysolepis* 105, *A. coelestinus* 78, *A. concolor* 74, *A. cooki* 70, *A. crassulus* 88  $\bar{x}$ , *A. cristatellus* 79, *A. cupreus* 88, *A. c. hoffmanni* 97, *A. c. macropophallus* 82, *A. c. spilomelas* 84, *A. cuprinus* 73, *A. cuvieri* 92, *A. cybotes* 77, *A. damulus* 110  $\bar{x}$ , *A. distichus* 87, *A. d. biminiensis* 90  $\bar{x}$ , *A. dolichocephalus sarmenticola* —, *A. d. portusalus* —, *A. dollfusianus* 94, *A. equestris* 93, *A. evermanni* 74, *A. extremus* —, *A. frenatus* 82, *A. fuscoauratus* 108, *A. f. kugleri* 102  $\bar{x}$ , *A. gadovii* 89, *A. garmani* 75, *A. gemmosus* 94, *A. grahami* 68, *A. g. aquarum* 73, *A. gundlachi* 69, *A. hendersoni* 84, *A. h. ravidormitans* —, *A. heteropholidotus* 109  $\bar{x}$ , *A. homolechis* 78, *A. h. cuneus* —, *A. h. jubar* —, *A. h. oriens* —, *A. h. quadriocellifer* —, *A. humilis* 105, *A. intermedius* 99, *A. isthmicus* 89  $\bar{x}$ , *A. kemptoni* 104, *A. krugi* 79, *A. lemurinus* 104, *A. limifrons* 103 (Costa Rica), *A.*

*limifrons* 99 (Pan.), *A. lineatopus* 69, *A. lionotus* 85, *A. lividus* —, *A. lysiana* 89  $\bar{x}$ , *A. luciae* —, *A. lucius* 84, *A. megapholidotus* 98, *A. mestrei* —, *A. monticola* —, *A. nebulosus* 100, *A. nigrolineatus* 94, *A. nubilus* —, *A. occultus* 100, *A. oculatus* —, *A. o. cabritensis* —, *A. o. montanus* —, *A. o. winstoni* —, *A. olsoni* 91, *A. opalinus* 82, *A. ortonii* 96  $\bar{x}$ , *A. pachypus* 101, *A. pentaprion* 81  $\bar{x}$ , *A. peraccae* 93  $\bar{x}$ , *A. petersi* +, *A. pinchoti* 90, *A. poecilopus* 96  $\bar{x}$ , *A. polylepis* 93, *A. poncensis* 87, *A. porcatus* 72, *A. pulchellus* 80, *A. punctatus* 88  $\bar{x}$ , *A. p. boulengeri* 103 m, *A. querorum* 89, *A. quadriocellifer* —, *A. richardi* 81, *A. ricordi subsolans* X, *A. r. viculus* —, *A. rodriguezi* 101, *A. roquet* 77, *A. rubribarbis* —, *A. rupinæ* —, *A. sabanus* —, *A. sagrei* 73, *A. s. stejnegeri* 79, *A. semilineatus* 86, *A. sericeus* 90, *A. smaragdinus* 78  $\bar{x}$ , *A. subocularis* 76, *A. stratulus* 86  $\bar{x}$ , *A. taylori* 79, *A. trachyderma* 115, *A. tropidogaster* 96, *A. tropidolepis* 99, *A. tropidonotus* 81, *A. uniformis* 98, *A. valencienni* 86, *A. villai* 89, *A. vittigerus* 125  $\bar{x}$ , *A. wattsi* 87, *A. woodi* 87  $\bar{x}$ , *Chamaeleolis chamaeleonides* 99, *Enyalioides laticeps* 108 m, *Enyalius bilineatus* ++, *E. boulengeri* +, *E. catenatus* X, *E. iheringii* ++, *Polychnerus marmoratus* 124  $\bar{x}$ , *Urostrophus ornatus* X.

Because the lizards of the genus *Anolis* are numerous in species and often extremely abundant, much information has accumulated concerning their sexual size relationships. Schoener (1967) noted that in *Anolis conspersus*, isolated from other species on Grand Cayman Island of the West Indies, males are much larger than females, and are able to take larger prey items of different kinds, with the result that there is partial partitioning of food resources between the sexes, and the potential carrying capacity of the habitat is increased. Later, Schoener (1970) discerned consistent patterns in the size relationships of insular West Indian species of *Anolis* of which there are several score. He found that wher-

ever a small island is inhabited by a single species, that species is small-sized (often 40-70 mm snout-vent), with males much larger than females. Thus the relationships found in *A. conspersus* were repeated in many other species. On islands that had two or more species, character displacement in size occurred to varying degrees. Depending on the extent of habitat overlap, species occurring in sympatry were altered from their size relationships in allopatric situations, becoming less similar, with SSD reduced so that size overlap with competing species was minimized. Schoener found that in solitary kinds, the males collectively are larger than the males on the island having the richest anole faunas. With increasing species diversity, the species size distribution of males irregularly decreases in median, but increases in range of skewness. He found greater SSD in larger species.

In a later study of mainland anoles I found (Fitch, 1976) correlation between climate and SSD; species living in relatively aseasonal climates of tropical rain forests or cloud forests tended to have the sexes nearly equal in size, or else the females were larger, but species living in sharply seasonal climates with drought or cold limiting reproduction to a concentrated short and stressful breeding season had males much larger than females (Table 6).

In *Anolis* species, SSD has a range

nearly as wide as that in all other lizards combined, with FMR from a minimum of 68 in *A. grahami* to 125 in *A. vittigerus*. Males are consistently larger than females in the insular species (mean FMR 81) whereas in about 40% of the mainland species females are larger (mean FMR 96). For 106 anole taxa FMR averages 89. It is noteworthy that no rainforest species of the mainland have males much larger than females. Similarly, in the giant rainforest anolines *Enyalioides*, *Enyalius*, *Polychrus*, and *Urostrophus*, females are relatively large.

**BASILISCINAE.** *Basiliscus basiliscus* 78, *B. vittatus* 86, *Corythophanes cristatus* 109  $\bar{x}$ .

In these amphibious and arboreal iguanids, SSD is large, and is accompanied by marked dimorphism, with dorsal crests developed in the male. Territoriality is highly developed in basilisks and males fight fiercely at times. In a study of Costa Rican populations of *B. basiliscus*, Van Devender (1978) found that SSD differed greatly, sometimes even between the populations of neighboring stream courses, and was highly responsive to such environmental factors as population density, and food supply.

**CROTAPHYTINES.** *Crotaphytus collaris* 93, *Gambelia wislizenii* 115. *C. collaris* is a fairly typical iguanid, having the male markedly larger than the female, territorial with bright colors and conspicuous display, whereas *G. wislizenii* is highly atypical, having the female much larger than the male, and the male lacking territoriality and display. *G. wislizenii* is nomadic, and a lizard may wander widely rather than remaining in a small and relatively permanent home range or territory such as found in most iguanids. Wandering tendencies are probably correlated with predatory habits; in addition to insects, leopard lizards regularly prey upon smaller lizards such as *Uta*, *Sceloporus*, *Phrynosoma* and *Holbrookia*. The large females are more saurophagous than the males. The allopatric *G. silus* of the San Joaquin Valley

TABLE 6. Mean Female to Male Ratios (FMR) in *Anolis*.

Species grouping	Number of taxa	Mean FMR	$\sigma^{in}$	Range
All species tested	106	89.21	$\pm 1.17$	(68-125)
Insular species	48	80.90	$\pm 1.15$	(68-100)
Mainland species (all)	58	96.09	$\pm 1.35$	(73-125)
Humid tropical lowlands	29	100.41	$\pm 1.78$	(81-125)
Montane	15	97.27	$\pm 1.84$	(87-110)
Xeric	12	85.00	$\pm 2.12$	(73-100)

in California differs from *G. wislizenii* in being largely insectivorous, in being territorial, and in having relatively large males.

IGUANINAE. *Amblyrhynchus cristatus* 85, *Conolophus subcristatus* 91 ♂, *Ctenosaura similis* 80, *Cyclura carinata* 82, *C. cornuta* 92, *C. cychlura* 93, *C. pinguis* 86, *Dipsosaurus dorsalis* 95, *Enyaliosaurus clarki* 93, *Iguana iguana* 91, *Sauromalus obesus* 92.

These mostly large to giant-sized, mainly herbivorous and mainly tropical iguanids all have males larger than females. Several of them have been subjects of intensive ecological and behavioral studies, which have indicated the following characteristics: there is a short and concentrated annual breeding season; males are highly territorial, but many are subordinates that are denied territories because they cannot compete with the dominant adults. Subordinate males are often adolescents or small adults that have not yet attained their prime. Reproductive females may be crowded together in harems, or may be spaced because of mutual intolerance much weaker than that prevailing among the males. The latter fight fiercely at times, but most often rely on their stereotyped displays to threaten or discourage potential rivals.

PHRYNOSOMINES. *Phrynosoma cornutum* 107, *P. coronatum* 102 X, *P. douglassi* 110, *P. modestum* 112 ♂, *P. orbiculare* 103 ♂, *P. platyrhinos* 106, *P. solare* 108.

The horned lizards are aberrant iguanids. Males lack bright colors and special display organs. Territoriality seems to be lacking and display is weakly developed. Whitford and Whitford (1973) found that individuals of *P. cornutum* often moved more than 100 meters in a day and frequently approached within one meter of another individual. Ordinarily when such lizards became aware of each other, there was head bobbing and mutual retreat. In an exceptional instance observed on 19 July 1972, one

lizard charged another that had approached, bit it, and secured a hold, and the two fought intermittently for an hour and 10 minutes until they were separated by the observer. Fighting consisted of biting, scratching, and thrusting movements of the head by which the opponent was jabbed with the occipital horns. Presumably the combatants were males, but their sex was not determined. Despite this isolated observation, it seems clear that display and combat behavior are relatively weak in *Phrynosoma* compared with those in most other iguanids. The horned lizards are largely myrmecophagous. They are relatively slow-moving and rely on their cryptic patterns and to a lesser extent on their spines for protection. Most of the species, including *cornutum*, *coronatum*, *modestum*, *platyrhinos*, and *solare* are oviparous, but *douglassi* and *orbiculare* are live-bearers. Broods in both the egg-laying and live-bearing species tend to be large compared with those of other iguanids of similar size. It is noteworthy that in all seven species investigated, females are larger than males, thus deviating from the usual trend in iguanids.

SCELOPORINAE. *Callisaurus draconoides* 89, *C. d. rhodostictus* 90, *Holbrookia maculata* 108, *H. m. approximans* 93 ♂, *Sceloporus adleri* 92, *S. bulleri* 97, *S. chrysostictus* 95, *S. clarki* 92, *S. c. boulengeri* 81, *S. cozumelae* 87, *S. cyanogenys* 105 ♂, *S. formosus* 103 ♂, *S. graciosus* 104, *S. g. "gracilis"* 103, *S. g. vandenburgianus* 95, *S. grammicus* 96, *S. insignis* 92, *S. jarrovi* 91, *S. lundelli* 105 ♂, *S. magister* 84, *S. malachiticus* 95, *S. megalepidurus* 99, *S. merriami* 95, *S. m. annulatus* 95, *S. mucronatus* 95, *S. nelsoni* 87, *S. occidentalis* 106, *S. o. biserratus* 107, *S. olivaceus* 111, *S. orcutti* 90, *S. pictus* 98 ♂, *S. poinsietae* 86, *S. pyrocephalus* 85 ♂, *S. scalaris* 111, *S. s. aeneus* 99, *S. s. bicarinatus* 106, *S. siniferus* 86, *S. smaragdinus* 93, *S. spinosus* 99, *S. tenuicnemis* 97, *S. teapensis* 93, *S. torquatus* 99 ♂, *S. undulatus* 110, *S. u. consobrinus* 101, *S. u. elongatus* 112, *S. u.*

*erythrocheilus* 110, *S. u. garmani* 107, *S. u. hyacinthinus* 107, *S. u. tristichus* 107, *S. uniformis* 93 ♂, *S. variabilis* 81, *S. virgatus* 112, *S. woodi* 106, *Uma inornata* 79, *U. notata* 79, *U. scoparia* 86, *Urosaurus ornata* 97, *Uta antiqua* 92, *U. mearnsi* 96, *U. nolascensis* 93, *U. palmeri* 91, *U. squamata* 93, *U. stansburiana* 87.

This is a large group of xeric adapted, mostly ground living (or scansorial), medium- to small-sized iguanids that are best represented in southwestern North America. Males are usually larger than females, but there are many exceptions, especially in the large genus *Sceloporus*. In most there is strongly developed sexual dichromatism with males having bright colors that function in aggressive displays. These colors are most often concentrated on the sides of the ventral surface, where they are concealed when the animal is at rest, flattened against the substrate. In some species display colors and behavior are largely lacking, and males do not maintain territories. In an earlier report (Fitch, 1978) I have discussed SSD in the genus *Sceloporus*. Those kinds having relatively large females were found to be characterized by a relatively large brood, single annual brood, small body size (< 60 mm S-V) and range in the Temperate Zone more often than by the opposite conditions. With few exceptions, most kinds of *Sceloporus* having females larger than males occur in the United States, north of latitude 30°, whereas most kinds having males larger occur south of latitude 30° in southern Texas, Mexico or Central America.

**TROPIDURINAE.** *Ctenoblepharis nigriceps* —, *Leiocephalus astictus* 85, *L. barbonensis* —, *L. b. aureus* —, *L. b. beatanus* —, *L. b. oxygaster* —, *L. cubensis* 77, *L. exotheotus* 84, *L. gigas* 72, *L. lunatus* —, *L. l. arenicolor* —, *L. l. melaenacelis* X, *L. l. thomasi* —, *L. macropus felinoi* 70 m, *L. pambasileus* 78 ♂, *L. paraphrus* 76 ♂, *L. personatus* —, *L. p. actitis* —, *L. p. agraulus* —, *L. p. budeni* —, *L. p. mentalis* —,

*L. p. scalaris* —, *L. p. tarachodes* —, *L. p. trujilloensis* —, *L. raviceps klinkowskii* 89 ♂, *L. r. uzzelli* 82, *L. sierrae* 66, *L. stictigaster* 83, *L. vinculum* —, *L. v. altavelensis* —, *Liolaemus anomalus* 91 ♂, *L. archeforus* 91, *L. a. sarmientiori* 94 m, *L. constanzae* —, *L. fuscus* —, *L. kingii* 92, *L. lemniscatus* —, *L. magellanicus* X, *L. monticola* X, *L. nigroviridis* —, *L. pictus* X, *L. platei* —, *L. tenuis* X, *Plica plica* X, *Plica umbra* 91 m, *P. u. ochrocollaris* 97 m, *Strobilurus torquatus* +, *Tropidurus albemarlensis* 79, *T. a. barringtonensis* 84, *T. bivittatus* 78, *T. delanonis* 76, *T. duncanensis* 89, *T. grayi* 116, *T. habeli* 79, *T. icae* 87, *T. occipitalis* 81, *T. pacificus* 87, *T. peruvianus* 86, *T. salinicola* 92, *T. stolzmanni* 71, *T. talarae* 78, *T. theresiae* X, *T. thoracicus* 87, *T. torquatus* 80 ♂, *Uracentron azureum* X, *U. a. guentheri* X, *U. a. werner* X, *U. flavigeckii* 70 ♂, *Uranoscodon superciliosus* X.

In this South American and West Indian subfamily males tend to be much larger than females (Fig. 1), and have display coloration and behavior well developed in connection with territoriality and courtship. An unexplained exception to this trend is *Tropidurus grayi* of Charles Island in the Galapagos, having females larger.

**AGAMIDAE.** *Agama agama* 86 m, *A. agilis* 87, *A. atra* —, *A. atricollis* 89 ♂, *A. cyanogaster* —, *A. hispida* 95 ♂, *A. h. aculeata* —, *A. kirki* —, *A. mossambica* —, *A. pallida* 109, *A. planiceps* —, *A. tuberculata* 93, *Amphibolurus maculosus* 91, *Calotes versicolor* —, *Draco melanopogon* 106, *D. quinquefasciatus* 102, *Gonocephalus modestus* —, *Japalura swinhonis* 95, *Leiolepis belliana* —, *Moloch horridus* 113, *Phrynocephalus ornatus* X, *P. scutellatus* 105 m, *Physignathus concinnus* —, *Salea anamallayana* —, *S. horsfieldi* —.

The agamids are active, diurnal, visually oriented lizards of Africa, Asia and Australia. Nearly all are oviparous. Various ecological studies of agamid species (Harris 1964, Mitchell 1973, Waltner

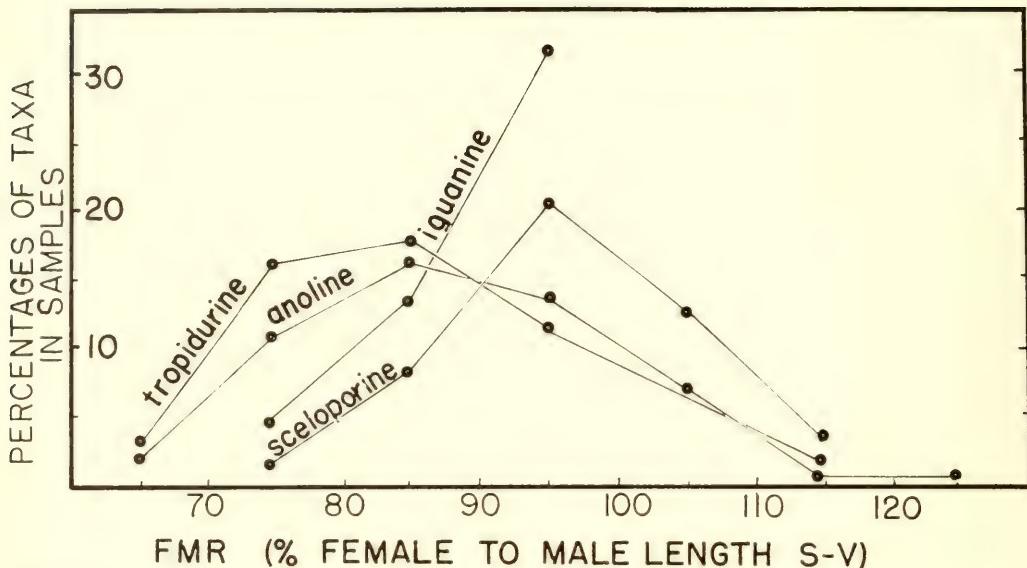


FIG. 1. Comparison of FMR in subfamilies of iguanid lizards; tropidurines and anolines especially tend to have relatively large males.

1978) have demonstrated that most agamids are highly territorial, with sexual dimorphism and special display organs in the male. Mitchell (1973) described the mating system in *Amphibolurus maculosus* in which only certain large and dominant males develop bright colors and maintain territories; others remain dull colored and passive and spend relatively little time above ground. Waltner (1978) observed male display and fighting in *Agama tuberculata*. He found FMR slightly lower (92.7) in a population at low altitude (having a relatively long active season and probably producing two clutches) than at medium altitude in the Himalayas where the season of activity was relatively short with only one clutch per year. Smith (1935) described male display and fighting in flying lizards (*Draco*). The males have distensible dewlaps and also have lateral patagia supported by the elongate ribs, used as wings to support the animals' weight in gliding but also having bright colors used in display. These lizards are often found in pairs and it has been suggested that they are monogamous but perhaps the associations

are temporary, as in many kinds of iguanids. The clutch in *Draco* is usually only two to four eggs. The Australian myrmecophagous desert agamid, *Moloch horridus* has relatively large females (FMR 113). It is solitary, non-territorial, nomadic, and slow-moving, relying on its spines and cryptic coloration for protection. It produces relatively large clutches (Pianka and Pianka, 1970). In all these traits it is remarkably convergent with the North American iguanid horned lizards (*Phrynosoma*).

**CHAMELEONIDAE.** *Chamaeleo adolfriederici* X, *C. anchetae* +++, *C. bitaeniatus* 101 ♂, *C. b. elliotti* ++, *C. b. graueri* X, *C. chapini* +++, *C. dilepis* 107 ♂, *C. d. idjwiensis* +, *C. etiennei* 109 ♂, *C. gracilis* X, *C. ituriensis* +, *C. johnstoni* X, *C. namaquensis* 106, *C. oweni* X, *C. pumilis* 107, *C. quilensis* 120, *C. roperi* +, *C. rufus* X, *C. senegalensis* ++, *Rhampholeon spectrum* X.

In this mainly African group specialized for arboreal existence, the males are territorial and may have special organs such as horns developed for fighting. Nevertheless available figures indicate that females are larger than males,

sometimes by a wide margin. There are both oviparous and viviparous species. Broods are large in both, but especially the former, which may produce clutches of several dozen eggs.

**ANGUIDAE.** *Anguis fragilis* +, *Anniella geronimensis* 94, *A. pulchra* 102 ♂, *Diploglossus costatus* —, *D. curtissi* —, *D. occiduus* —, *D. stenurus* —, *D. warreni* —, *Gerrhonotus monticolus* 94, *G. moreleti* 93 ♂, *G. multicarinatus* 98, *G. m. webbii* 98, *Ophisaurus attenuatus* 95, *Wetmorena haetiana mylica* X, *W. h. surda* X.

In these serpentiform lizards the sexes are similar in most respects, but in *Gerrhonotus* and *Ophisaurus* the males have wider head and bulging temporal muscles, and the strong jaws serve for fighting in the breeding season. It is probably significant that females are larger than males in the more subterranean kinds such as European "slow worm," *Anguis*.

**LACERTIDAE.** *Acanthodactylus cantoris* 87, *Aporosaura anchietae* 90 m, *Eremias argus* +, *E. arguta* 93 m, *E. breviceps* —, *E. burchelli* +, *E. capensis* —, *E. guttulata* 99 ♂, *E. lineoocellata* X, *E. lugubris* 96 ♂, *E. namaquensis* 90 ♂, *E. savagei* 98, *E. undata* X, *Ichnotropis bivittata* —, *I. capensis* 95, *I. squamulosa* 95 ♂, *Lacerta agilis* 108 m, *L. a. chersoneensis* 100 m, *L. melisellensis* 88, *L. muralis* 102 m, *L. m. maculiventris* 99 m, *L. pratincola* 116 m, *L. sicula* 90, *L. s. alveaoi* 92 m, *L. s. ciclopica* 94 m, *L. s. medemi* 88 m, *L. taurica* 82 m, *L. tiliqua* —, *L. t. eiselti* 91 ♂, *L. t. maresi* 90 ♂, *L. t. pardii* —, *L. trilineata* 105, *L. t. media* 103, *L. vauverselli* 102 ♂, *L. viridis* 93, *L. v. chlornota* 92 ♂, *L. vivipara* 116 m, *L. wagleriana* 92 m, *L. w. antoninoi* 87 ♂, *L. w. maritlinensis* 88 m, *Meroles cuneirostris* 91 m, *Nucras delalandii* X, *N. tessellata* —, *Scapteira knoxi* —, *Tropidosaura gularis* X.

The active, diurnal, Afro-Eurasian lizards of this family are all oviparous with the single exception of *Lacerta vivipara*. There is often some sexual

dichromatism, and males have wider heads with more massive jaw muscles. Males are aggressive and quarrelsome. FMR averaged  $95.1 \pm 1.45$  in 32 kinds, and 22% had females that averaged larger than males. In *Lacerta* the range of SSD was found to be unusually large, from 116 and 112 in *L. pratincola* and *L. vivipara* to 82 in *L. taurica*.

**TEIIDAE.** *Alopoglossus atriventris* 106 m, *A. copii* 111 ♂, *Ameiva ameiva* 95, *A. auberi* 83, *A. chaitzami* —, *A. festiva* 86, *A. quadrilineata* 97 m, *A. undulata* 84, *A. u. amphigramma* X, *A. u. gaigeae* —, *A. u. hartwegi* —, *A. u. parva* —, *A. u. podarga* —, *Arthrosaura kockii* 107, *A. reticulata* 86 m, *Bachia flavesiensis* (= *cophias* 108 ♂, *vermiforme* 99 m), *B. trinasa* 104 ♂, *Callopistes maculatus* —, *Cercosaura ocellata* 103 m, *Cnemidophorus bacatus* 92 ♂, *C. calidipes* 91 ♂, *C. deppei* 93, *C. d. infernalis* —, *C. guttatus* 93 ♂, *C. g. flavolineatus* —, *C. hyperythrus* 97, *C. inornatus* 104, *C. lemniscatus* 79, *C. lineatissimus* 89, *C. l. duodecimlineata* —, *C. parvisocius* 91, *C. sacki* 93 m, *C. sexlineatus* 101, *C. tigris* 94, *Iphisa elegans* 100 ♂, *Kentropyx calcaratus* 97, *K. pelviceps* 96 m, *K. striatus* 89, *Leposoma guianensis* 103 ♂, *L. parietale* 105, *Neusticurus bicarinatus* 85, *N. cochranae* +, *N. equeleopus* 93, *N. rufus* X, *N. strangulatus* —, *N. tatei* —, *Opipenter xestus* +, *Pholidobolus affinis* —, *P. macbrydei* X, *P. montium* ++, *P. prefrontale* +, *Prionodactylus argulus* 100, *P. manicatus* 123 ♂, *Proctoporus boliviensis* 106, *Ptychoglossus brevifrontalis* 111 m, *Tretioscincus agilis* 107, *Tupinambis nigrolineatus* ——.

The teiids are oviparous New World lizards of varied habits and small to large size. Most are tropical. *Ameiva*, *Cnemidophorus*, *Kentropyx*, *Tupinambis* and a few other genera comprise the macroteiids, relatively large, active, primarily terrestrial types, whereas the microteiids are small and many are secretive, fossorial, or arboreal. Active competition with fighting, for prospective mates, food, shelter, or other resources is com-

mon in macroteiids, but is not known to occur in microteiids. In the latter the females are most often the larger (12 of 18 species, mean FMR 103).

Figures are available for 20 species of macroteiids and in all but two, males were the larger, FMR averaging 92 for the entire group (Fig. 2). Macroteiids are diurnal. Chasing and fighting are prominent aspects of behavior wherever population densities are high. In most instances those activities seem not to involve territorial defense, as many individuals may share the same small area, with overlapping ranges. Fighting probably establishes dominance or priority in mating.

Macroteiids conform to a widespread trend in that the lowest FMRs are all of tropical species, whereas the two species having the females larger than males both inhabit the Temperate Zone.

Clutches tend to be larger in the Temperate species which oviposit only once or a few times annually, but smaller in tropical kinds that breed throughout the annual cycle or a major part of it. The need to produce large clutches would in turn select for large body size in the females.

**SCINCIDAE.** *Ablepharus kitaibelii* 115 m, *A. smithii* X, *A. wahlbergii* 111  $\bar{x}$ , *Brachymeles gracilis* 93 m, *Cryptoblepharus boutoni* 102, *Emoia adspersa* 101, *E. atrocostata* 97, *E. baudini* X, *E. cyanura* 99, *E. lawesii* 102, *E. nigra* 94, *E. samoensis* 94, *Eumeces brevirostris* 104  $\bar{x}$ , *E. copei* +, *E. dugesii* X, *E. egregius* 106, *E. fasciatus* 99, *E. gilberti* 90, *E. g. cancellus* 97, *E. g. placerensis* 95, *E. g. rubricaudatus* 102, *E. inexpectatus* 98, *E. latiscutatus* 98, *E. obsoletus* 102, *E. ochoterenae* 102  $\bar{x}$ , *E. septentrionalis* 101  $\bar{x}$ , *E. skiltonianus* 101, *E. s. utahensis* 104,

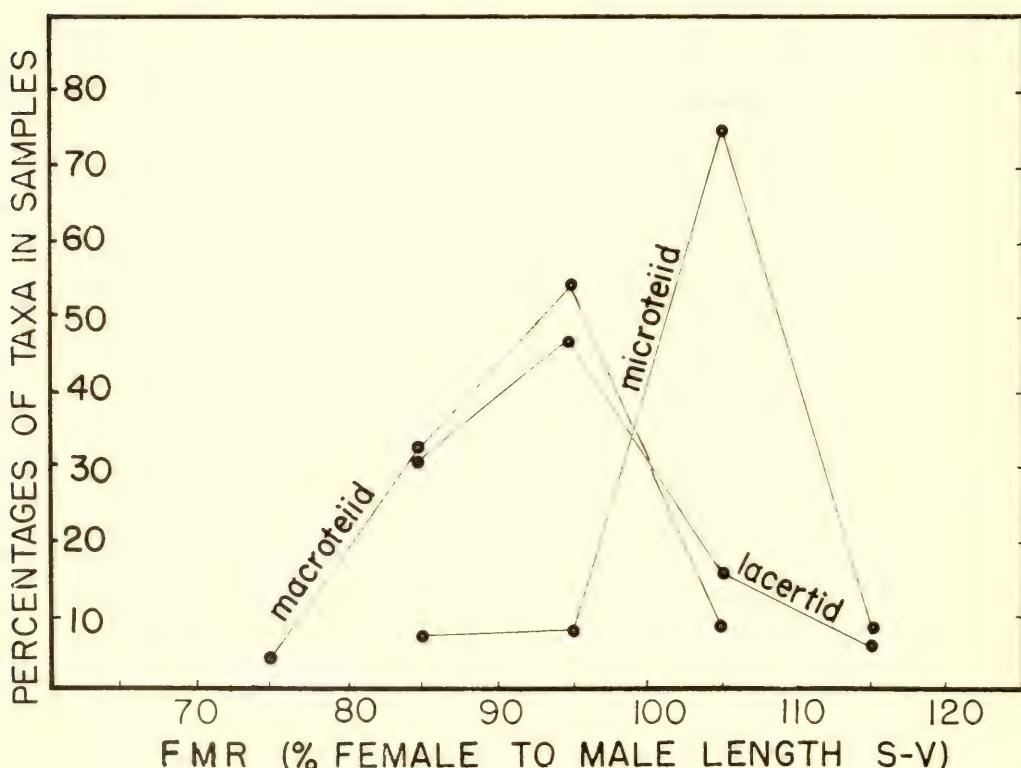


FIG. 2. Comparison of FMR in teiids and lacertids; most microteiids differ from most macroteiids and lacertids in having relatively large females.

**Leioploisma rhomboidalis** 100, **Lipinia noctua** 101, **Lygosoma graueri** +, **L. kilimense** +, **L. luberoensis** -, **L. solomonis** -, **Mabuya bayoni** 105  $\bar{x}$ , **M. brachypoda** 101  $\bar{x}$ , **M. buettneri** 120  $\bar{x}$ , **M. capensis** X, **M. lacertiformis** +, **M. mabouya** 112, **M. m. alliacea** 106  $\bar{x}$ , **M. maculata** 96, **M. maculilabris** 98, **M. megalura** +++, **M. multifasciata** 94 m, **M. occidentalis** 108  $\bar{x}$ , **M. perroteti** -, **M. punctata** 88, **M. quinquetaeniata** ++, **M. q. margaritifer** 88  $\bar{x}$ , **M. q. obsti** X, **M. rufus** X, **M. sparsa** 87, **M. spilogaster** 104, **M. striata** 101, **M. s. chimbawa** +, **M. s. ellenbergi** X, **M. sulcata** +, **M. varia** 106  $\bar{x}$ , **M. variegata** 111  $\bar{x}$ , **Ophiomorus persicus** 119  $\bar{x}$ , **O. rathmai** 112  $\bar{x}$ , **O. tridactylus** 103  $\bar{x}$ , **Riopa anchetae** ++, **R. sundevalli** X, **Scincella lateralis** 105, **S. reevesi** ++, **Scincus hemprichii** --, **S. mitratus** 79  $\bar{x}$ , **S. scincus** 85, **Sepsina tetradactyla** ++, **Sphenomorphus cherriei** 100, **S. megaspila** +, **Typhlosaurus garipensis** 106, **T. lineatus** 105.

Of 52 skinks for which definite FMRs are available, 31 had females larger, 19 had males larger and 2 had nearly equal-sized sexes (Fig. 3). FMR ranged from 79 to 120, mean 101.0  $\mp$  1.15. Both *Eumeces* and *Mabuya* were found to be divided between species having the male larger and those having the female larger, but the latter group was somewhat more numerous. In secretive and burrowing skinks especially (*Ophiomorus* and *Typhlosaurus*), there is a tendency for females to be relatively large, and presumably male rivalry and combat is less developed among those kinds that spend most of their time underground. Among those kinds with subterranean tendencies, clutch size is reduced sometimes to only one egg, but egg size is correspondingly large.

**XANTUSIIDAE.** *Xantusia henshawi* 111, *X. h. bolsoni* +. In the gecko-like, viviparous granite night lizard the sexes are similar in appearance but females are markedly larger. Probably both sexes maintain territories. There are two young at a birth.

**CORDYLIDAE.** *Cordylus capensis* X, *C. coeruleopunctatus* X, *C. giganteus* X, *C. jonesi* +, *C. jordani* X, *C. polyzonus* +, *C. tropidosternum* X, *C. vandami* +, *C. warreni* ++, *Gerrhosaurus flavigularis* X, *Platysaurus capensis* X, *P. guttatus* -, *P. intermedius* -, *P. mitchelli* X, *Pseudocordylus microlepidotus* X, *P. wilhelmi* ---.

These armored African lizards usually live in rocky places. *Cordylus* is viviparous. Seemingly the group as a whole has females larger than males with some exceptions to this trend in *Platysaurus* and *Pseudocordylus*.

**VARANIDAE.** *Varanus acanthurus* 87  $\bar{x}$ , *V. komodensis* ----. The monitors range from small size up to the three meters of the giant Komodo dragon lizard. All are oviparous. The larger kinds are formidable predators. Male fighting has been observed in various species. The two species for which size data are available indicate that males are markedly larger than females.

### Squamata: Amphisbaenia

**AMPHISBAENIDAE and TROGONOPHIIDAE.** *Amphisbaena alba* 103, *A. fuliginosa* 97 m, *Blanus cinereus* 100, *Trogonophis wiegmanni* 98  $\bar{x}$ .

The few figures available for these wormlike reptiles indicate that the sexes are approximately the same size. There is no mention of sexual size difference in the many papers by Gans and others on amphisbaenians.

### Squamata: Serpentes

**Serpentes. (Henophidia).**

**ACROCHORDIDAE.** *Acrochordus javanicus* +++.

**ANILIDAE.** *Anilius scytale* +++.

**BOIDAE.** *Candoia aspera* +++, *C. carinata* 137, *Charina bottae* 112  $\bar{x}$ , *C. b. utahensis* 122  $\bar{x}$ , *Corallus caninus* +, *C. enydris* X, *Epicrates angulifer* +++, *E. cenchria* 114  $\bar{x}$ , *E. fordii* --,

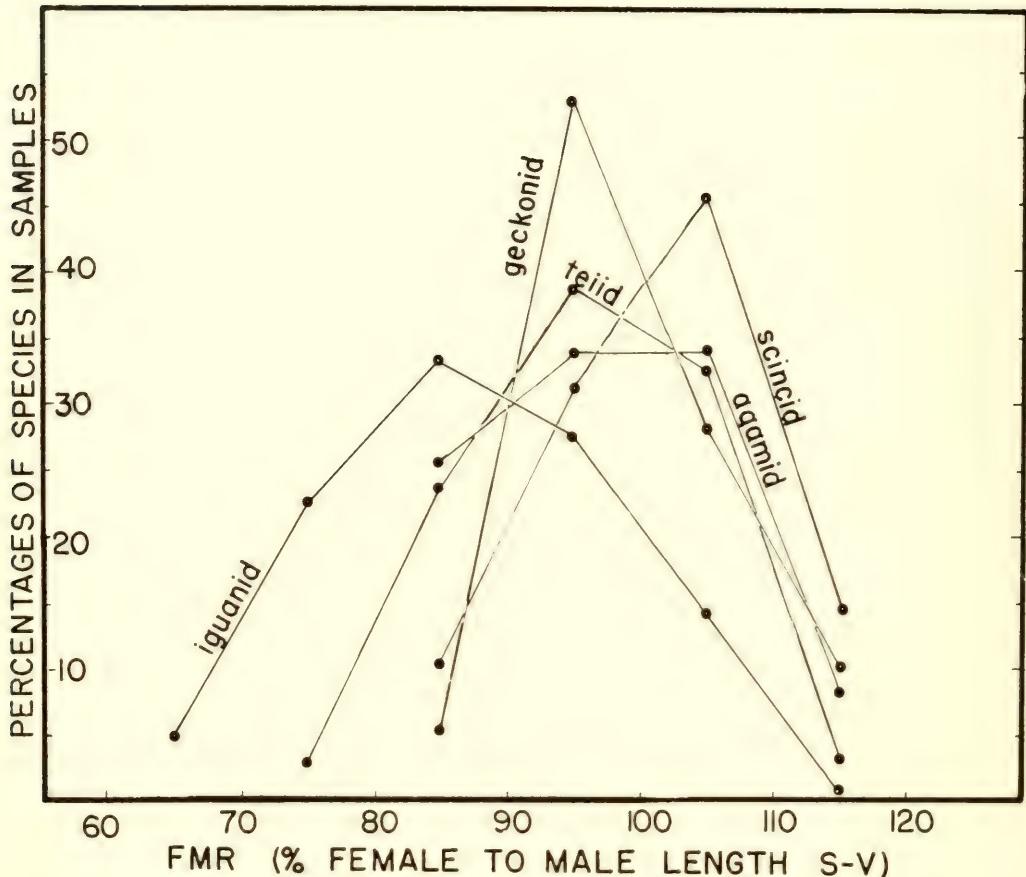


FIG. 3. Comparison of FMR trends in several families of lizards; in most species of iguanids, males are larger than females, whereas skinks tend to have relatively large females.

*E. gracilis* X, *E. striatus* —, *Eryx conicus* +++, *E. johni* +, *Python sebae* +++, *Tropidophis haetianus* X, *T. nigrovittatus* +.

**UROPELTIDAE.** *Rhinophis drummondhayi* +++, *R. philippinus* —.

**XENOPELTIDAE.** *Xenopeltis unicolor* ++.

In these primitive snakes, the hennophidians, of five families, including the highly aquatic *Acrochordus*, and the somewhat fossorial anilids, uropeltids, xenopeltids and *Charina*, it seems to be the general rule that the females are larger. In some of them the size difference between the sexes is large. These snakes are ecologically diverse. Most of the kinds listed are viviparous. Barker et al. (1979) have described male combat

in *Python molurus*. Four males confined with a female fought frequently. Fighting consisted of crawling over the opponent, gouging him with the erected pelvic spurs, and biting. As a result of such encounters the males arranged themselves in a social hierarchy. Mating success was highly correlated with success in combat and position in the hierarchy. As the breeding season waned, combat ceased. Combat has been reported in one other boid, the arboreal *Sanzinia madagascariensis* (Carpenter et al., 1978).

**Serpentes (Scolecophidia).**

**TYPHLOPIDAE.** *Typhlops angolensis adolfi* 125, *T. a. dubius* 136 ♂, *T. a. iraci* 141 ♂.

The figures for this African species

indicate that in the wormlike blind snakes, as in most other fossorial reptiles, females are substantially larger than males.

### Serpentes (Caenophidia).

**COLUBRIDAE.** This is by far the largest family of living snakes. Figures are available for 202 taxa classed as colubrids; in 71% of these, females were found to be larger than males, in 4% the sexes were approximately equal and in 25% males were larger. The colubrids are so diverse ecologically that few general statements apply well to the group as a whole.

Relationships among the host of colubrid genera and species are still poorly understood and existing classifications are controversial. For convenience in discussing SSD in colubrids, they are divided into subfamily groupings, following the system presented by Smith, Smith and Sawin (1977).

**ALSO PHIINAE.** *Arrhyton dolichurum* —, *A. taeniatum* +, *A. vittatum* —, *A. v. landoi* +, *Atractus* "species A" +, *A. badius* ++, *A. carrioni* 142 ♂, *A. elaps* 111, *A. latifrons* +++, *A. major* 111, *A. multicinctus* 110 ♂, *A. occipitoalbus* 126 ♂, *A. resplendens* +, *A. roulei* ++, *Clelia rustica* 97 ♂, *Farancia abacura* 165 m, *F. a. reinwardti* 159 m, *F. erythrogramma* 149, *Oxyrhopus melanogenys* 115 ♂, *O. petola* 118, *O. trigeminus* +++, *Tachymenis chilensis assimilis* 87 ♂, *T. c. melanura* 106 ♂, *T. peruviana* 93, *Uromacer catesbyi* ++, *U. c. insulaevaccirum* +++, *U. c. frondicator* +++, *U. c. hariolatus* ++, *U. c. inchausteguii* +++, *U. c. pampineus* +++.

These New World and mainly tropical colubrids are a diverse assemblage, with a wide range of sizes, habitats, and strategies of feeding and reproduction. Some are highly prolific; eggs average more than 30 per clutch in both species of *Farancia*. Females are larger than males in most, and attain maximum relative size in *Farancia*. However, males may be larger than females in *Clelia*

and *Tachymenis*. In examining extensive series of *Conophis*, Wellman (1963) found females to be larger in *C. lineatus dunni* and *C. pulcher* but found males to be larger in *C. l. lineatus*, *C. l. concolor*, and *C. vittatus*.

For 14 alsophiines a mean FMR of  $120.64 \pm 6.61$  was obtained.

**APARALLACTINAE.** *Amblyodipsas polylepis* +++, *A. unicolor* 150 ♂, *A. ventrimaculatus* ++, *Aparallactus capensis* +, *A. guentheri* +, *A. jacksoni* X, *A. lunulatus* 131 ♂, *A. modestus* 120 ♂, *A. ubangensis* ++, *A. ulugurensis* X, *Microleps boettgeri* +++, *Miodon christyi* +++, *M. collaris* +++, *M. c. graueri* +, *Xenocalamus mechowi* +++, *X. sabiensis* ++. The available evidence indicates that females are larger, often by a wide margin, in the snakes of this African subfamily.

**ATRACTASPINAE.** *Atractaspis bibroni* 111 ♂, *A. congica* —, *A. dahomeyensis* +, *A. irregularis* 110 ♂, *A. microlepidotus* —, *A. m. fallax* X, *A. m. micropholis* —.

These "false vipers" have only recently been reallocated as colubrids. They resemble viperids in having long, folding poison fangs and a fairly potent venom. Neither sex is consistently larger but in some the sexes are approximately equal, while the maximum size attained is greater in females of some kinds and in males of others.

**BOIGINAE.** *Ahaetulla mycterizans* +++, *A. nasuta* +++, *A. prasina* 122 ♂, *A. pulverulenta* +++, *Boiga blandingii* +, *B. ceylonensis* +++, *B. cyanea* +++, *B. cynodon* ++, *B. dendrophila* 96 ♂, *B. forsteni* —, *B. gokool* +, *B. multimaculata* +++, *B. ochracea* +, *B. pulverulenta* 106 ♂, *B. trigonata* ++, *Crotaphopeltis degeni* X, *C. hotamboeia* 105, *Dipsadoboaa duchesnei* —, *D. elongata* —, *D. unicolor* 84 ♂.

These are Asiatic and African rear-fanged snakes, mostly of arboreal habits. In the Asiatic *Ahaetulla* and *Boiga* females are larger than males, but in the African *Crotaphopeltis* the sexes are

nearly equal-sized and in *Dipsadoboaa* males are larger.

**BOODONTINAE.** *Boaedon fuliginosus* +++, *B. lineatus* 140  $\bar{x}$ , *B. olivaceus* X, *Grayia ornata* ++, *G. smythii* X, *G. tholloni* +++, *Lampropolis aurora* +++, *L. inornatus* +++, *Lycodonomorphus laevissimus* +++, *L. leleupi* +++, *L. rufulus* ++.

In these African "house snakes" and "swamp snakes" females average much larger than males.

**CALAMARINAE.** *Calamaria agamensis* 118, *C. gervaisi* 126  $\bar{x}$ , *C. leucogaster* +, *C. linnaei* ++, *C. lumbricoidea* 115, *C. modesta* ++, *C. multiplicata* 126, *C. pavimentata* 116  $\bar{x}$ , *C. septentrionalis* ++, *C. uniformis* +, *C. virgulata* 116, *Trachischium fuscum* +++, *T. guentheri* +++, *T. laeve* +++.

In these small, secretive or fossorial Oriental snakes, females average consistently larger than males.

**COLUBRINAE.** *Argyrogena fasciolata* X, *Arizona elegans* X, *Chironius carinatus* —, *C. fuscus* —, *Coluber constrictor* 110, *C. jugularis* 71 m, *C. karelini* ++, *C. raverieri* —, *C. spinalis* 126  $\bar{x}$ , *C. ventromaculatus* —, *C. viridiflavus* 86  $\bar{x}$ , *C. v. xanthurus* 77, *Coronella austriaca* 102, *C. brachyura* —, *Drymoluber dichrous* 74, *Elaphe climacophora* 102, *E. conspisillata* 100  $\bar{x}$ , *E. dione* 103  $\bar{x}$ , *E. flavolineata* 104  $\bar{x}$ , *E. helena* +++, *E. hodgsoni* —, *E. longissima* 86 m, *E. obsoleta* 96, *E. porphyriaca* 100  $\bar{x}$ , *E. quadrivirgata* 92, *E. radiata* 108  $\bar{x}$ , *E. taeniura* ++, *Elapoides fuscus* 110, *Gongyllosoma baliodeira* 108, *Gonyosoma oxycephala* +, *Leptophis ahaetulla* 91, *Liopeltis calamaria* ++, *L. frenatus* —, *L. rappi* X, *L. scriptus* X, *L. stoliczkae* —, *Lytorhynchus diadema* —, *Masticophis lateralis* 106, *M. taeniatus* 95 m, *M. t. ruthveni* 96 m, *Meizodon coronatus* +, *M. semiornatus* +++, *Opheodrys aestivus* 100 m, *O. major* 83  $\bar{x}$ , *O. multicinctus* —, *O. vernalis* 101  $\bar{x}$ , *Pituophis melanoleucus affinis* 104, *P. m. catenifer* 95 m, *P. m. deserticola* 91, *P. m. sayi* 101, *Ptyas korros* 92, *P. mucosus* 94, *Salvadora*

*grahamiae* X, *S. hexalepis* 90 m, *S. h. mojavensis* 84 m, *S. h. virgultea* 91 m, *S. lemniscata* 97, *S. mexicana* 87, *Spalerosophis cliffordi* 107, *S. diadema* ++.

The snakes of this almost cosmopolitan subfamily are medium-sized or large, active, diurnal, and with few exceptions are egg-layers. Some are constrictors; some are arboreal but most are terrestrial. They differ from the majority of snakes in tending to have males larger than females, but there is much difference between genera and species in this regard. Among 37 taxa males were larger in 23, sizes were equal in 3 and females were larger in 11. In these 37 taxa for which substantial series were available FMR averaged  $96.0 \pm 1.40$ . In the North American racer, *Coluber constrictor*, females are considerably larger than males (FMR 110), but in some of the Old World species of *Coluber* the opposite relationship applies, FMR 71 in *C. jugularis*, and 77 in *C. viridiflavus xanthurus*. Probably male aggression or combat occurs to some degree in all of these snakes. It has been known since ancient times in at least the aesculapian snake *Elaphe longissima*; the caducis which symbolizes the medical profession, is a representation of male combat in this species (FMR 87). Rigley (1971: 65) first described male combat under natural conditions in *Elaphe obsoleta*. Two of the snakes were lying with their tails and posterior parts of their bodies intertwined while the anterior parts were swaying and looping. Each seemed to be striving to hold down and press against the ground the head and forebody of the opponent. Stickel, Stickel and Schmid (1980) observed male combat twice in their 22-year study of a rat snake population. There was spiral twisting of the bodies as each snake seemed to be striving to keep its head in a superior position and force its opponent to the ground. Once the aggressor bit the other snake. One encounter lasted three minutes and the other 45 minutes. One of the same snakes was

involved in both encounters. Bogert and Roth (1966) described male combat in the gopher snake (*Pituophis melanoleucus*).

DASYPELTINAE. *Dasypeltis atra* +++, *D. fasciata* ++, *D. scabra* 117 ♂.

The African egg-eaters differ from other snakes in morphological features associated with their specialized feeding habits. Their relationships are uncertain. Females are relatively large.

DIPSADINAE. *Carphophis vermis* 117, *Coniophanes bipunctatus* +++, *C. fissidens* 114, *Diadophis punctatus* 111, *Dipsas catesbyi* 96, *D. pavonina* —, *D. variegata* X, *Ficimia olivacea* 95 ♂, *Ficimia quadrangularis* 95, *Geophis brachycephalus* 117 m, *G. hoffmanni* 132 m, *G. nasalis* 105 m, *G. rhodogaster* 124 m, *G. semidoliatus* 129 m, *Gyalopion canum* 106, *Hypsiglena torquata* +++, *Imantodes cenchoa* 109 ♂, *Leptodeira annulata* 108, *L. a. ashmeadi* ++, *L. a. cussiliris* +++, *L. a. rhombifera* ++, *L. frenata* ++, *L. nigrofasciata* +, *L. polysticta* ++, *L. punctata* +, *L. septentrionalis* +++, *L. s. ornata* +++, *Pseustes poecilonotus* +, *Rhadinea brevirostris* —, *R. calligaster* +++, *R. decorata* +, *R. flavidata* 112, *R. fulvittis* +, *R. gaigeae* ++, *R. hesperis* +++, *R. laureata* ++, *Sibon dimidiata* ——, *S. nebulata* X, *S. n. leucomelas* X, *S. sannio* —, *Sibynomorphus mikani* ++, *S. ventrimaculatus* +, *Tantilla gracilis* 126, *T. melanocephala* +, *T. planiceps* 94 m, *Tretanorhinus nigroluteus* 141, *Trimorphodon biscutatus lambda* 130 ♂, *T. b. vandenburghi* 127 m, *T. b. lyrophantes* +.

The dipsadines are New World snakes that are mostly medium-sized or small, nocturnal and/or secretive-fossorial, predatory on invertebrates such as earthworms, slugs, snails, and soft-bodied insects, or on frogs, and in a few cases, on lizards or small snakes. Most are tropical. All are oviparous. Females were found to be larger than males in 16 of the 19 species for which series were available, but *Sibon* is an exception to this general trend. FMR aver-

aged  $114.32 \pm 2.85$ . To my knowledge, male combat or rivalry has not been recorded in any dipsadine.

DISPHOLIDINAE. *Dispholidus typus* 102 ♂, *Telescopus dhara* +++, *T. semiannulatus* 128 ♂, *Thelotornis capensis* 100 ♂, *T. kirtlandi* +. These are arboreal African rear-fanged snakes, the boomslangs, large-eyed snakes and twig snakes. Females tend to be larger than males.

GEODIPSANAE. *Geodipsas depressiceps* 116 ♂, *Psammodynastes pulverulentus* 109 ♂.

The mock vipers and their relatives are rear-fanged terrestrial Old World snakes. Females are larger than males. In *Psammodynastes* there is color dimorphism in the sexes.

HOMALOPSINAЕ. *Cerberus rhynchops* 118 ♂, *Enhydris chinensis* +, *E. bocourti* +++, *E. enhydris* 109, *E. plumbea* +, *Fordonia leucobalia* 119 ♂, *Homalopsis buccata* 109.

These heavy-bodied viviparous rear-fanged snakes occur in freshwater or estuarine habitats of southeastern Asia and the Indo-Australian Archipelago. They have usually been placed in a family separate from the Colubridae. Females are consistently larger than males.

HYDROPSINAЕ. *Helicops angulatus* ++. Like other groups of aquatic snakes, this Neotropical genus has females larger than males.

LAMPROPELTINAE. *Cemophora coccinea* 79 ♂, *Lampropeltis calligaster* 91, *L. getulus* 87, *L. g. boylii* 95, *L. g. holbrookii* 88, *L. multicincta* 112 m, *L. pyromelana* 91 m, *L. triangulum* 88 ♂, *L. t. elapoides* 88 ♂, *L. t. syspila* 97, *Rhinocheilus lecontei* 87 m, *R. l. "clarus"* 91 m, *R. l. tessellatus* —, *Stilosoma extenuatum* 104 m. In these oviparous North American constrictors males are usually larger than females (FMR averaged  $91.5 \pm 1.90$  for 13 taxa). Male competition and combat has been noted in various kinds of king snakes. An excellent account of fighting in *L. calligaster* was that of Moehn (1967). Two males were

found engaged in a "combat dance." They were captured and caged together, and fighting continued intermittently over a period of days. It involved rearing and attempting to throw down the opponent with coiling and jerking movements, but also involved pursuit and vicious biting.

**LYCODONTINAE.** *Dinodon flavozonatum* 83 ♂, *D. orientale* 100 m, *D. rufozonatum* 96 ♂, *Lycodon aulicus* +, *L. jara* +, *L. subcinctus* +, *L. travancoricus* +.

These are nocturnal, oviparous, Asiatic snakes; *Dinodon* species average considerably larger than those of *Lycodon*. The limited data available indicate that the females are larger in *Lycodon*, but males tend to be larger in *Dinodon*.

**LYCOPHIDIINAE.** *Lycophidion variegatum* +, *L. capense* 133 ♂, *L. laterale* X, *L. ornatum* +++, *L. semiannule* X, *Mehelya capensis* ++, *M. poensis* +++, *M. savorgnanii* ++, *M. stenophthalmus* +++, *Natriciteres olivacea* 125 ♂.

The wolf snakes, file snakes and marsh snakes of this subfamily are African and tend to nocturnality and to lizard- or frog-eating habits. To varying degrees the females are larger than the males.

**NATRICINAE.** *Amphiesma beddomei* +++, *A. craspedogaster* +, *A. khasiensis* +, *A. modesta* +++, *A. monticola* +++, *A. platiceps* -, *A. popei* X, *A. pryeri* +++, *A. sauteri* 116 ♂, *A. sieboldi* +++, *A. stolata* 133, *A. venningi* +, *A. vibakari* X, *A. xenura* X, *Aspidura copi* +, *A. trachyprocta* +++, *Atretium schistosum* 120 ♂, *Balanophis ceylonensis* -, *Clonophis kirtlandi* 110 m, *Haplocercus ceylonensis* X, *Macropisthodon plumbicolor* +++, *M. rudis* 139 m, *Natrix annularis* 138, *N. natrix* 114 m, *N. n. sicula* 115, *N. percarinata* 136 ♂, *N. tessellata* 103 m, *N. trianguligera* 118, *Nerodia cyclopion* 124 m, *N. erythrogaster bogerti* 107 ♂, *N. e. transversa* 115, *N. fasciata* 116 m, *N. f. clarki* +++, *N. f. confluens* 132 m, *N. f. pictiventris*

152 m, *N. rhombifera* 111, *N. r. blanchardi* 120, *N. r. werleri* 162, *N. sipedon* 132, *N. s. insularum* 108 m, *N. s. pleuralis* 124 m, *N. taxispilota* 117 m, *N. valida* 135, *N. v. celaeno* 109, *N. v. isabelleae* 142, *N. v. thamnophisoides* 121, *Opisthotropis latouchi* +, *Pseudoxenodon macrops* -, *P. nothus* -, *Regina alleni* 106 m, *R. grahami* 120, *R. rigida* 134 m, *R. septemvittata* 114, *Rhabdophis auriculata* +, *R. a. myersi* ++, *R. chrysargia* 106, *R. himalayana* +++, *R. nigrocincta* X, *R. nuchalis* +++, *R. subminiata* 122, *R. tigrina* 120, *Rhabdops bicolor* +, *Seminatrix pygaea* 110, *Storenia dekayi texanum* 120, *S. d. victa* 120, *S. occipitomaculata* 118, *Thamnophis brachystoma* 112 m, *T. butleri* 109, *T. couchi* 132 m, *T. c. gigas* 134 m, *T. c. hammondi* 136 m, *T. c. hydrophilus* 130 m, *T. cyrtopsis* 146 m, *T. elegans* 118 m, *T. e. biscutatus* 138 m, *T. e. terrestris* 106 m, *T. e. vagrans* 122, *T. eques* 115 ♂, *T. marcianus* 126 m, *T. ordinoides* 125, *T. proximus* 110, *T. radix* 108 m, *T. rufipunctatus* ++, *T. sauritus* 118, *T. sirtalis* 114, *T. s. parietalis* 123, *T. s. pickeringi* 124, *Tropidoclonion lineatum* 122, *Virginia striatula* 116, *V. valeriae* 124, *Xenochrophis cerasogaster* 153 ♂, *X. piscator* 135, *X. punctulata* ++, *X. vittata* 124, *Xylophis perroteti* ++.

This large subfamily of holarctic colubrids, including the water snakes, garter snakes and their relatives, are active, diurnal or nocturnal, and many have aquatic or wetland habitats. They are mostly medium-sized or small, and feed on a variety of vertebrate and invertebrate prey, but especially on fish. In general, members of this group are "r-selected," with rapid development, large clutches or litters and rapid population turnover. All species in the nine North American genera are live-bearers, whereas the much more diverse Asiatic species are oviparous, with the single exception of *Natrix annularis*. Regardless of these differences, it is a general rule that females are larger but *Pseudoxenodon* is an apparent exception. In

63 taxa for which definite figures were available, FMR averaged  $122.05 \pm 1.52$  (Fig. 4). It averaged 122 for 20 kinds of *Thamnophis* (Table 7) and 124 for 13 kinds of *Nerodia*. In various natricines mating aggregations have been observed, with complete lack of male rivalry. Several males may simultaneously court the same female, their massed bodies forming a "snake ball." With no rivalry or combat between males, large male size would confer no selective advantage, but large size in the female enables her to produce a relatively large clutch or litter. Primiparous females are much smaller and less prolific than others, but successive broods become progressively larger as the female gains in bulk.

TABLE 7. Mean Female to Male Ratios (FMR) in *Thamnophis*.

Species grouping	Number of taxa	Mean FMR	$\sigma^{in}$	Range
All species tested	20	122.30	$\pm 2.50$	(106-146)
Aquatic species	6	136.00	$\pm 2.31$	(130-146)
Marshland species	9	118.00	$\pm 2.31$	(108-126)
Terrestrial species	5	114.00	$\pm 3.38$	(106-125)

#### NOTHOPSINAE. *Ninia maculata* 107 $\bar{x}$ .

In the diminutive and secretive Neotropical "coffee snake" females are larger than males.

OLIGODONTIDAE. *Holarchus violaceus* 87  $\bar{x}$ , *Oligodon barroni* +, *O. catenata* X, *O. cinereus* +, *O. cruentatus* ++, *O. cyclurus* --, *O. melaneus* -, *O. splendidus* X, *O. taeniatus* X, *O. taeniolatus* +, *Phylorhynchus browni* -, *P. decurtatus nubilus* 110 m, *P. d. perkinsi* 97.

Size relationships of the sexes are variable in this group including the Asiatic oligodonts and the North American leaf-nosed snakes.

PAREATINAE. *Pareas carinatus* 100, *P. margaritophorus* +++, *P. monticola* +++.

These are slender, short-headed, nocturnal, often arboreal snail-eating snakes of southeastern Asia and nearby islands. Females considerably exceed male size in some.

PHILOTHAMNINAE. *Chrysopelea paradesi* 124  $\bar{x}$ , *Dendrelaphis picta* 114  $\bar{x}$ , *Gastrophysix smaragdina* ++, *Philothamnus heterodermus* +, *P. hoplogaster* 120  $\bar{x}$ , *P. inornatus* ++, *P. irregularis* 133  $\bar{x}$ , *P. natalensis* ++, *P. ornatus* +++, *P. semiornatus* X, *P. semivariiegatus* 103  $\bar{x}$ , *Thrasops jacksoni* 126  $\bar{x}$ .

This small subfamily includes the

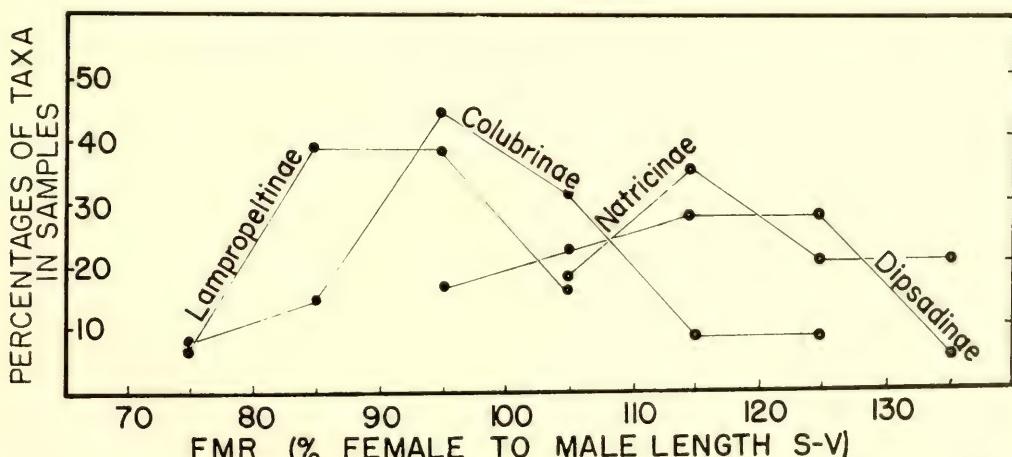


FIG. 4. Comparison of the trends of FMR in four subfamilies of colubrid snakes; females are larger than males in most dipsadines and natricines, whereas the reverse size relationship exists in most colubrines and lampropeltines.

"flying snakes" of southeastern Asia, and the green snakes and tree snakes of Africa. All are active and arboreal, feeding on lizards and sometimes on birds. Females are larger than males.

**PSAMMOPHIINAE.** *Hemirhagerrhis nototaenia* 105 ♂, *Psammophis angolensis* +, *P. crucifer* X, *P. jallae* —, *P. punctulatus* —, *P. schokari* 77 m, *P. sibilans* 82, *P. subtaeniatus* —, *Psammophylax tritaeniatus* 93 ♂, *Rhamphiophis acutus* 87 ♂.

The African bark snakes, sand snakes, and skaapstekers of this group are mainly terrestrial and diurnal rear-fanged colubrids. Seemingly males are substantially larger than females in most members of the group, especially in the genus *Psammophis*.

**PSEUDASPINAЕ.** *Duberria lutrix* 118 ♂, *D. rhodesiana* +++, *D. variegata* +++, *Prosymna ambigua* 117 ♂, *P. bivittata* +++, *P. jani* ++, *P. lineata* —, *P. sundevallii* +++, *Pseudaspis cana* X.

This African subfamily includes the diminutive, viviparous slug-eaters, water snakes, the fossorial shovel-nosed snakes, and the large, viviparous, rodent-eating mole snake. Of the latter, FitzSimons (1962) wrote that ". . . males have been observed to fight fiercely and gnash each other severely with their teeth." However, the entire group seems to be characterized by relatively large females.

**SONORINAE.** *Sonora episcopa* 100, *S. michoacanensis* 104 ♂, *S. semiannulata* 99.

In these small and secretive North American snakes, the FMR is near parity; either females or males may be slightly larger. Male combat has been described in *S. episcopa* by Kroll (1971). In a group of the snakes captured in mid-March and confined together, fighting was observed on 17, 19 and 20 March. It involved biting an opponent and intertwining with him, and was associated with mating. Males were observed to interrupt their courtship to attack a second male that approached the pair.

**XENODONTINAE.** *Heterodon nasicus* 125 ♂, *Xenodermus javanicus* 111.

These small colubrids of southeastern Asia are predatory on frogs and invertebrates. Females are larger than males.

**XENODERMATINAE.** *Achalinus spinalis* 116 m, *H. platyrhinos* 107 m, *Leimadophis reginae* 112, *L. taeniurus* 105 ♂, *Liophis miliaris* 124, *Xenodon rabdocephalus* ++, *X. severus* 96. These are small to large New World snakes that feed largely on toads, frogs and invertebrates. The few available records suggest that females are usually larger than males, or if males are larger the disparity is small.

**ELAPIDAE.** *Aspidelaps scutatus* +, *Bungarus bungaroides* —, *B. candidus* —, *B. fasciatus* —, *B. multicinctus* —, *B. walli* —, *Calliophis calligaster* —, *C. c. gemianulus* —, *C. japonicus* —, *C. maclellandi* +++, *C. maculiceps* ++, *Dendroaspis angusticeps* X, *D. jaimesoni* +, *D. polylepis* X, *Elapsoidea guentheri* X, *E. loveridgei* —, *E. l. colletti* +, *E. semiannulata* X, *Hemichatus hemichatus* +++, *Laticauda colubrina* +++, *L. laticauda* ++, *Maticora intestinalis* 99 ♂, *Micrurus alleni* ++, *M. fulvius* 134, *M. f. tenere* 119, *M. langsdorffi* +, *M. nigrocinctus* +++, *M. spixii* —, *Naja haje* —, *N. melanoleuca* 85 ♂, *N. mossambica* X, *N. naja* 99, *N. n. samarensis* +, *N. nigricollis* 102 ♂.

Although the Australian proteroglyphs are no longer considered elapids, the group still includes highly diverse genera of American, African and Asiatic snakes, and may be polyphyletic. Within the group, medium to large size and snake-eating habits are common. All except *Hemichatus* are oviparous. In *Hemichatus* FMR is especially high, and for the group as a whole the usual condition seems to be that of having the females larger. The Asiatic coral snakes and kraits, *Bungarus* and *Calliophis*, are exceptions, having males larger than females. The primitive oviparous seasnakes or "sea kraits" of the genus *Laticauda* are now considered elapids not closely

related to hydrophiine seasnakes (Smith et al., 1977). In *Laticauda* females are larger than males.

**HYDROPHIIDAE.** This family is now construed to include not only the true sea snakes (hydrophiines) but also the primitive terrestrial Australian proteroglyphs that have formerly been considered elapids (oxyuranines; Smith et al., 1977). The two subfamilies are much different ecologically, and their representatives are therefore listed and discussed separately.

**HYDROPHIINAE.** *Astrotia stokesii* +++, *Enhydrina schistosa* 111 ♂, *Hydrophis brookei* X, *H. caerulescens* —, *H. cyanocinctus* ++, *H. fasciatus* —, *H. klossi* +, *H. lapemoides* X, *H. mammillaris* X, *H. obscurus* +, *H. ornatus* —, *H. spiralis* +, *H. stricticollis* X, *H. torquatus* 97 ♂, *Kerilia jerdoni* 103 ♂, *Lapemis curtus* 100, *Microcephalus cantoris* ++, *M. gracilis* +, *Pelamis platurus* 118, *Praescutata viperina* —, *Thalassophis anomalus* —.

The sea snakes are medium-sized to large viviparous, marine, fish-eaters. Compared with terrestrial snakes they are less prolific, having only one or two young at a birth in some instances. Even in the tropical climates where most occur, there is a brief annual breeding season. Large-scale mating aggregations have been observed (Smith, 1943). Apparently mating is promiscuous in these aggregations. There are no records of male competition or combat.

Of the 20 species for which information is available, five apparently have males larger than females, five have the sexes about equal and 10 have females larger than males. Large series are available to compare sizes of the sexes only in *Enhydrina schistosa*, *Lapemis curtus* and *Pelamis platurus*. In the latter species Kropach (1975) found a mean length S-V of 452 mm in 359 males and 481 mm in 391 females, FMR 109, but the series included immatures as well as adults. Kropach also listed the lengths of 100 of the largest individuals and found 70

were females. Means for the 30 largest of each sex were utilized to calculate FMR of 118.

**OXYURANINAE.** *Acanthophis antarcticus* 131, *Austrelaps superbus* 92, *Cacophis kreftii* 112, *C. harriettae* 125, *C. squamulosus* 129, *Hemiaspis signata* 99, *Notechis scutatus* 99, *Pseudechis porphyriacus* 95, *Urechis gouldi* 83, *Vermicella annulata* 139.

The Australian proteroglyphs, perhaps more than any other snakes, are noted for male combat. Worrell (1964) described this behavior as follows:

Coinciding with the mating season is the spectacular wrestling of the males . . . . One or more males may pursue each other over rocks, through creeks and scrub, twining around each other, wrestling and crawling frenziedly about the bush, flattening the grass as they writhe, and stopping occasionally to lift their forebodies high, swaying nervously.

It is significant that of the species checked, only those of the small secretive *Cacophis* and *Vermicella* and the sluggish, viperlike *Acanthophis* were found to have females larger than males. Male combat has not been observed in these two genera, and probably does not occur. Shine (1980c) emphasized the viperlike appearance, behavior, and reproductive and feeding strategy of the Australian death adder as a case of evolutionary convergence.

**VIPERIDAE.** *Atheris nitschei* ++, *A. squamiger* 113 ♂, *Bitis arietans* 93, *B. caudalis* X, *B. cornutus* —, *B. gabonica* ++, *B. nasicornis* +++, *B. paucisquamata* +, *B. peringueyi* ++, *Causus defilippii* X, *C. lichtensteini* 115 ♂, *C. lineatus* +, *C. resimus* +, *C. rhombatus* 95 ♂, *Cerastes cerastes* 120 ♂, *Echis carinata* 129 m, *E. colorata* 98, *Pseudocerastes fieldi* 108 ♂, *Vipera ammodytes* 118 m, *V. berus* 108, *V. latastei* 90 ♂, *V. superciliaris* +, *V. ursini* 110, *V. xanthina* 95.

These are venomous front-fanged snakes of Africa and Eurasia. Most are heavy-bodied and slow-moving, securing their prey by ambush and the venomous

bite. For 13 species FMR averaged 107 (90-129). Most species have females larger than males, and most are viviparous, producing medium to large litters. Relatively large size of the female makes possible the production of large litters. However, there is male combat in vipers, and in fact males of *Vipera berus* are known to be territorial. In a study of the diminutive *V. ursini*, Bruno (1967a) found that FMR increased from 104 in Yugoslavia to 105 in Italy and 110 in France. The Yugoslavian vipers were found to be the largest and the Italian were the smallest. St. Gurons (1978) noted that the sexes are about the same size in *Vipera aspis* and probably in *V. kaznakovi*, whereas males are the larger in *V. ammodytes* and females are larger in *V. berus*, *V. seoanei* and *V. ursini*. All these are small vipers of cold and temperate climates of Europe and Asia.

**CROTALIDAE.** *Agkistrodon acutus* +, *A. blomhoffi brevicaudus* X, *A. b. sinicus* X, *A. caliginosus* X, *A. cognatus* -, *A. contortrix* 94, *A. halys* 112 X, *A. himalayanus* X, *A. piscivorus* 96, *A. rhodostoma* ++, *A. saxatilis* -, *Bothrops atrox* 115, *B. bilineatus* ++, *B. lansbergi* 101, *B. nasutus* 96, *B. neuwiedii* X, *B. pulcher* 153 X, *B. punctatus* 144 X, *B. schlegelii* 111, *Crotalus atrox* 91, *C. cerastes* 103, *C. durissus* 88, *C. d. terrificus* 97, *C. enyo* 92, *C. horridus* 94, *C. lepidus* 82 X, *C. l. klauberi* 85, *C. lucassensis* 87, *C. mitchelli* 94, *C. m. pyrrhus* 78, *C. m. stephensi* 88, *C. molossus* 91, *C. m. nigrescens* 84, *C. pricei* 82, *C. ruber* 84, *C. scutulatus* 88, *C. tigris* 82, *C. triseriatus* 90, *C. viridis* 92, *C. v. concolor* 88, *C. v. helleri* 80, *C. v. lutosus* 90, *C. v. nuntius* 78, *C. v. oreganus* 87, *Hypnale hypnale* ++, *H. walli* -, *Sistrurus catenatus* 92, *S. rarus exiguus* 76 X, *Trimersurus albolabris* 161 X, *T. cantoris* +++, *T. elegans* X, *T. erythrurus* +++, *T. flavomaculatus* +++, *T. flavoviridis* 89, *T. gramineus* +++, *T. jerdoni* ++, *T. kaulbacki* +, *T. labialis* +, *T. macrolepis* +++, *T. malabaricus* +++, *T. microsquamatus* X, *T. monti-*

*cola* +++, *T. okinavensis* 99, *T. puniceus* 139 X, *T. purpureomaculatus* +++, *T. stejnegeri* 109 X, *T. strigatus* +, *T. tokarensis* --, *T. trigonocephalus* +++, *T. wagleri* X.

The pit vipers are now generally considered to be a subfamily of the Viperidae. These New World and Asiatic sole-noglyphs are mostly medium-sized to large, heavy-bodied and slow-moving ambush hunters, predatory on vertebrates. They rely on potent venom to subdue the prey. Most are live-bearers, but a few Asiatic species of *Agkistrodon* and *Trimersurus* as well as the Neotropical *Lachesis* are oviparous. In most species of *Trimersurus* females are markedly larger than males, but males are larger than females in 24 of 25 kinds of rattlesnakes. The exception is *Crotalus cerastes* in which FMR is 103 and for the entire group FMR averages  $87.6 \pm 1.19$  (Table 10). Females are relatively small in *C. mitchelli pyrrhus* (77) and *C. viridis nuntius* (78) whereas in *C. molossus nigrescens* the ratio is near parity (99). There is no obvious correlation with body size, nor with climate. Rival male rattlesnakes approach each other, rear with their ventral surfaces in contact, and with sudden jerky motions each attempts to throw down its opponent. The larger and heavier snake is usually the winner but sometimes only after a prolonged bout; the loser withdraws from the encounter and leaves the area. Large size in the male would seem to confer selective advantage. Whether some species of rattlesnakes are more inclined to rivalry and combat than others is still unknown.

In the copperhead *Agkistrodon contortrix* and the cottonmouth *A. piscivorus*, the FMRs 93 and 96 were similar to those found in rattlesnakes. Both these species are known to have a combat dance, similar to that of rattlesnakes except in details. Whether the same applies to the Asiatic species is not known, but published figures on maximum sizes indicate that in some of them the fe-

males are the larger including *A. blomhoffi siniticus*, *A. acutus* and *A. halys*. Males are the larger in *A. halys cognatus*, *A. saxatilis* and *A. blomhoffi brevicaudus*, while in *A. caliginosus* the sexes seem to be equal. In the Asiatic *Hypnale walli* males are the larger. In the Neotropical *Bothrops* and the Asiatic *Trimeresurus* females are usually much larger than males.

### Crocodylia

**CROCODYLIA.** *Alligator mississippiensis* 82, *Crocodylus niloticus* 85.

The alligator was studied in Louisiana by Chabreck and Joanen (1979) from 2500 young captured, marked and released, and 218 recoveries, some after attainment of adult size. The data indicated that in both sexes growth continued long after sexual maturity, but at reduced rates, slowing earlier and more abruptly in the female. The following average total lengths in meters were calculated or projected:

10-year-olds	males 2.55	females 2.10
20-year-olds	males 3.50	females 2.55
oldest	males 4.2	females 2.73

At the age of ten years, both males and females were sexually mature but still growing rapidly; at age 20 females were near their maximum size but males were still capable of substantial gain. FMR was 82 for 10-year-olds, 73 for 20-year-olds and 65 for the oldest. The latter is one of the lowest FMR figures recorded for reptile species.

Cott (1961) indicated the following total lengths and weights for mature *Crocodylus niloticus*:

Males (14)	3.416 m (3.073-3.743)
	170.8 kg (115.8-240.0)
Females (50)	2.911 m (2.600-3.192)
	104.2 kg (70.2-146.2)

In this crocodile SSD is large, but less than in *Alligator mississippiensis*. Probably males are substantially larger than females in most crocodilians, with similar trends of widening SSD with advancing age, but definite figures are not

available. Staton and Dixon (1977) in a study of *Caiman crocodylus* observed instances of coitus in which males appeared to be 1.7 to 2.5 m in length and females 1.2 to 1.5 m. However, Brazaitis (1973) noted that in the small *Alligator sinensis* the female is larger than the male. Presumably this was mentioned because it is the exception, and size relationships of the sexes were not indicated for other kinds of crocodilians in Brazaitis' review.

Crocodilians are known to maintain territories, and male aggression and combat are common. Garrick and Lang (1977) compared social behavior in *Alligator mississippiensis*, *Crocodylus acutus* and *C. niloticus*. They found that in all three species combat between males contesting for dominance precedes the establishment of mating territories. Voice is prominent in social behavior. Both sexes "bellow," especially in the breeding season. The bellowing alligator is usually in the water. The sound is accompanied by stereotyped movement with raising of the head and arching of the tail, and, in the male, eversion of the submaxillary gland. Bellowing signals the presence and location of the individual as a member of a social group (Garrick, Lang and Herzog, 1978). Territorial males dominate the breeding groups. In *A. mississippiensis* alpha males have been observed to interrupt courtship of subdominants. Females show submissive behavior in the presence of territorial males but may form dominance hierarchies among themselves. They move freely from one male's territory to another.

Selective factors which might tend to increase female size in crocodilians are: (1) large clutch size, and the need to increase the capacity of the female; (2) Cannibalistic predation on the dependent young, and the need for maternal defense against other adults, including males. Factors which might select for increased male size are direct competition for females, or for breeding ter-

ritories, and the existence of social hierarchies. Stress associated with breeding and competition for mates is intensified because it is concentrated in a relatively short breeding season in all species.

## DISCUSSION

Extensive sampling, comparing sizes of the sexes in many species of reptiles, has demonstrated SSD to be extremely labile within the class. Females ranged in size from just over one-fourth to about 15 times male bulk in a virtual continuum. Within each of the main groups, turtles, lizards and snakes, also, was found a wide range of SSD, and to a lesser degree the same statement applied to families, subfamilies and genera (Tables 8 to 11). Even individual species proved to have important differences in SSD from one population to another, and seemingly SSD is highly susceptible to selective pressure bringing about evolutionary change. Also, direct environmental influences may alter SSD.

In turtles and snakes it is most common for females to exceed males in average size, whereas in lizards the opposite relationship is more common. However, in each group many exceptions from the

general trend are found and these aid in identifying some of the factors which were the basis for natural selection producing sexual size differences. Rivalry and aggression in males promote selection for large individuals of that sex; selection for large clutches or litters, and for relatively large neonates may result in selection of relatively large females.

The seven reptile species noted as having the lowest FMRs, 70 or less (minimum 66) are all insular West Indian iguanids, *Anolis* (5 species) and *Leiocephalus* (2 species). It has already been shown under the discussion of *Anolis*, that relative size of females averages markedly smaller in the insular species than in those of the mainland. This condition is associated with generally high population densities, light predation pressure, and intense intraspecific competition in the insular species. Divergence in sizes of the sexes alleviates intraspecific competition for food (Schoener, 1967).

One of the seven species with lowest FMR, *Anolis lineatopus* (FMR 69) of Jamaica has been the subject of an intensive ecological study (Rand, 1967). These findings are of special interest

TABLE 8. Distribution Of FMR Percentages Within The Turtles, Lizards, Snakes And Major Families Of These Groups.

	Number of taxa	Female length as percentage of male length (FMR)								
		<80%	80-89%	90-99%	100%	101-110%	111-120%	121-130%	>130%	Total
Turtle	50	—	4%	18%	8%	20%	8%	2%	40%	100%
Emydid	28	—	—	11%	7%	14%	11%	—	57%	100%
Lizard	408	11%	21%	33%	2%	27%	6%	1%	—	100%
Geckonid	43	—	5%	26%	9%	51%	9%	—	—	100%
Iguanid	226	20%	27.5%	31%	1%	17%	2.5%	1%	—	100%
Agamid	12	—	25%	34%	—	33%	8%	—	—	100%
Lacertid	32	—	19%	56%	3%	16%	6%	—	—	100%
Teiid	38	3%	18%	37%	5%	29%	5%	3%	—	100%
Scincid	51	2%	8%	26%	4%	46%	14%	—	—	100%
Snake	278	2.5%	11.5%	19%	3%	19%	20.5%	12%	12%	100%
Colubrid	214	—	7.5%	14%	3%	19.5%	22.5%	14%	12.5%	100%
Elapid-hydrophiid	21	—	9%	33%	5%	10%	19%	10%	4%	100%
Viperid	13	—	—	38%	—	23%	31%	8%	—	100%
Crotalid	41	7%	34%	34%	—	8%	7%	—	10%	100%

because *A. lineatopus* is suspected to be representative of various other lizards that have relatively large males and small females in its social system and reproductive strategy. As in other anoles, the females lay one egg per clutch, but oviposition is frequent and breeding occurs throughout the year. Hatchlings are intolerant of each other and from the start they space themselves and defend territories. However, they avoid adults and are subject to cannibalistic predation. Individuals of both sexes and all sizes are territorial, but agonistic behavior is directed mainly against similar-sized individuals. Hence, territories may overlap extensively. An adult female may have several mutually exclusive juveniles living within her territory. Small lizards avoid larger ones, and are generally ignored or sometimes briefly chased by them. A male's territory may encompass those of several females and he may mate with them regularly. Males spend much of their time in territorial display. One male observed for an entire day displayed on the average, every 3.5 minutes. However, there is little precopulatory display or courtship. Females are individually recognized. Mating occurs when an approached female is receptive and does not move away to avoid the male. Nonreceptive females flee and escape the male easily. Imma-

ture males may compete with similar sized females for territories. Also, they may be treated as females by courting adult males, but invariably flee from the male's approach. On the average males use larger and higher perches than do other individuals. Although displays usually serve to maintain territorial spacing, rival males fight fiercely at times. Combat usually involves threatening approach, sparring, and biting with jaws interlocked. Usually one combatant is thrown from perch to ground. Combats usually are brief and do not result in serious injury to either participant.

Forty-four additional species of reptiles were found to have notably low FMRs in the range from 71 to 80. These included seven species of snakes (*Crotalus*, *Coluber*, *Cemophora*, *Drymoluber*, *Psammophis*, *Sistrurus*) but were mostly lizards. The latter included a skink (*Scincus*) and a teiid (*Cnemidophorus*) but otherwise were all iguanids, especially species of *Anolis* (15 insular, 5 mainland), *Leiocephalus* (4 insular) and *Tropidurus* (4 insular, 3 mainland), but also including *Uma* (2) and *Ctenosaura* (1).

For some of these species habits are little known, but a few have been subjects of intensive field study. In an early study of *Anolis sagrei* (FMR 79) in Cuba, Evans (1938) described territoriality and

TABLE 9. Distribution Of FMR Percentages Within Major Subfamilies Of Iguanid Lizards And Colubrid Snakes.

	Num- ber of taxa	Female length as percentage of male length (FMR)								Total
		<80%	80-89%	90-99%	100%	101- 110%	111- 120%	121- 130%	>130%	
Iguanidae	226	20%	27.5%	31%	1%	17%	2.5%	1%	—	100%
Anolinae	115	26%	28%	21%	2%	17%	4%	2%	—	100%
Iguaninae	11	—	36%	64%	—	—	—	—	—	100%
Sceloporinae	62	3%	18%	50%	—	23%	6%	—	—	100%
Tropidurinae	33	33%	42%	18%	—	—	3%	—	—	100%
Colubridae	214	—	7.5%	14%	3%	19.5%	22.5%	14%	12.5%	100%
Alsophiinae	14	—	7%	14%	—	14%	29%	7%	29%	100%
Colubrinae	36	8%	14%	33%	8%	33%	—	3%	—	100%
Dipsadinae	20	—	—	20%	—	20%	25%	25%	10%	100%
Lampropeltinae	13	8%	38%	38%	—	8%	8%	—	—	100%
Natricinae	66	—	—	—	—	18%	35%	20%	27%	100%

male fighting. He found a social system in which dominant adult males maintained large territories supporting various other categories of individuals including juveniles, breeding females, and subordinate males. Michael (1972) studied the ecology of *Anolis carolinensis* (FMR 79) in eastern Texas. He found that most females begin to ovulate in the season following their own hatching. Although males attain sexual maturity early, when they are less than a year old, still relatively small, and lacking full development of their secondary sexual

characters, nearly all matings involve the relatively few large and dominant males that are at least 36 months old and 60 mm S-V. In *Cnemidophorus lemniscatus* (FMR 79) males are more brightly colored than females, and are known to be fierce fighters.

*Ctenosaura similis* (FMR 80) also has a polygynous mating system, with large dominant males having relatively large territories which may each include the territories of several females. The latter are mutually exclusive, but the females are less agonistic than males. Immature or subordinate adults may have territories within those of other individuals. *Ctenosaura* is an exception to the rule that most reptiles that have relatively small females have small egg clutches (e.g., only one egg in *Anolis*). A large female ctenosaur may lay more than 80 eggs; average clutch was found to be 43 (Fitch and Henderson, 1978).

The snakes that have exceptionally low FMRs are rattlesnakes, and colubrids of two subfamilies. The spectacular combat dance of the rattlesnakes is well known. Many of the field observations of it pertain to *Crotalus mitchelli* and *C. viridis*, the two species having the lowest FMR (78 in both *C. m. pyrrhus* and *C. v. nuntius*). The existence of male combat in *Drymoluber dichrous* (FMR 74) and *Psammophis*

TABLE 10. Mean Female to Male Ratios (FMR) For Species In Various Genera Of Lizards And Snakes.

Genus	Num- ber of taxa	Mean FMR	$\sigma_m$	Range
<i>Anolis</i>	106	89.21	$\pm 1.17$	( 68-125)
<i>Cnemidophorus</i>	12	93.08	$\pm 1.79$	( 79-104)
<i>Crotalus</i>	25	87.60	$\pm 1.19$	( 78-103)
<i>Elaphe</i>	9	99.00	$\pm 2.24$	( 86-108)
<i>Eumeces</i>	14	99.93	$\pm 1.11$	( 90-106)
<i>Lacerta</i>	22	96.27	$\pm 1.97$	( 82-116)
<i>Lampropeltis</i>	9	93.10	$\pm 2.64$	( 87-112)
<i>Leiocephalus</i>	11	78.36	$\pm 2.12$	( 66- 89)
<i>Mabuya</i>	16	101.56	$\pm 2.42$	( 87-120)
<i>Nerodia</i>	17	125.11	$\pm 3.81$	( 107-162)
<i>Phyllodactylus</i>	12	101.25	$\pm 1.48$	( 95-115)
<i>Sceloporus</i>	49	97.96	$\pm 1.23$	( 81-112)
<i>Sphaerodactylus</i>	7	107.00	$\pm 1.90$	( 99-113)
<i>Thamnophis</i>	20	122.30	$\pm 2.50$	( 106-146)
<i>Tropidurus</i>	16	84.38	$\pm 2.52$	( 71-116)

TABLE 11. Distribution Of FMR Percentages Within Various Genera Of Snakes And Lizards.

	Num- ber of taxa	Female length as percentage of male length (FMR)								Total
		<80%	80-89%	90-99%	100%	101- 110%	111- 120%	121- 130%	>130%	
<i>Anolis</i>	106	28%	29%	21%	1%	18%	1%	1%	-	100%
<i>Cnemidophorus</i>	12	4%	4%	67%	-	25%	-	-	-	100%
<i>Crotalus</i>	25	8%	54%	33%	-	4%	-	-	-	100%
<i>Eumeces</i>	14	-	-	43%	-	57%	-	-	-	100%
<i>Lacerta</i>	22	-	24%	41%	4%	24%	9%	-	-	100%
<i>Leiocephalus</i>	14	36%	36%	28%	-	-	-	-	-	100%
<i>Mabuya</i>	16	-	19%	19%	-	43%	19%	-	-	100%
<i>Nerodia</i>	17	-	-	-	-	18%	29%	18%	35%	100%
<i>Phyllodactylus</i>	12	-	-	31%	23%	38%	8%	-	-	100%
<i>Sceloporus</i>	49	-	17%	48%	-	27%	8%	-	-	100%
<i>Thamnophis</i>	20	-	-	-	-	20%	25%	30%	25%	100%
<i>Tropidurus</i>	16	38%	50%	6%	-	6%	-	-	-	100%

*schokari* (FMR 79) may be suspected. Social interactions between snakes are much less often observed than those of lizards. Aggressive behavior has been reported in relatively few kinds but perhaps occurs in many others. Presumably those males that are most aggressive and most successful in vanquishing rivals in the combat dance are also most successful in mating, but this relationship has not actually been demonstrated in field studies.

The possibility of males siring offspring by forcible mating may have led to selection for larger size in the male. Even a small difference in size between the sexes with the male larger and stronger, might greatly increase the possibility of rape. In a species having the female larger, she would tend to dominate and intimidate the male; he could not overpower her and rape would scarcely be possible. Thornhill (1980) has developed the theory that large male size has evolved in many species, including humans, to make rape possible. He rejected the idea that sexual dimorphism in humans was related to an evolutionary history in which the prevalent mating system was harem polygyny, but ". . . regardless of the prevalent mating system in human evolutionary history, larger males were favored because of the increased likelihood of successful rape if they failed to compete successfully for parental resources."

In both snakes and turtles the highly altered body form renders copulation difficult, and even though the male succeeded in overpowering the female, he might not be able to accomplish intromission. In both groups female cooperation seems essential for consummation of courtship to occur. A female tortoise may frustrate the male's attempts merely by resting her shell on the substrate instead of standing, and a female snake must raise her tail causing the cloaca to gape for the male's hemipenis to be inserted. In contrast, lizards accomplish copulation much more readily. Seem-

ingly forcible copulations, including homosexual matings with subordinate or defeated males, are fairly common. It may be significant in this connection that the male is the larger in the majority of lizard species, whereas the reverse is true in the majority of snakes and turtles.

Predation may be an important inhibition to the development of male combat and the evolution of relatively large males. In discussing sexual size differences in amphibians, Shine (1979) wrote that

. . . a major factor in the evolution of male combat may be the participant's vulnerability to predation. Fighting frogs are exposed to predators . . . and one might expect combat to be most common in species that are at little risk. Risk should be lowest in species with large body size or chemical defenses . . .

Presumably the same factors affect sexual size ratios in reptiles. In snakes, especially, male fighting and relatively large male size are characteristic of formidably venomous kinds—rattlesnakes and their near relatives, and the Australian oxyuranines. Although none of these snakes is free from predation, they are certainly much less vulnerable than non-venomous types, and hence can indulge in fighting with reasonably low risk of predation. Male fighting and relatively large male size is also conspicuous in the crocodilians, giant reptiles which as adults are generally secure from predation.

In lizards, on the contrary, male fighting and relatively large male size is common and occurs mostly in kinds that are not large or formidable and lack noxious qualities—lacertids, teiids and iguanids (especially anolines and tropidurines) that are highly vulnerable to predation. A common trait of these species is that they are active, agile and swift. A combat or chase may be almost instantaneous, and exposure to predation is thereby minimized for any single encounter. Likewise, in snakes, several of

those that have relatively large males and are known or presumed to have male combat are relatively innocuous but fast-moving kinds, *Coluber* and *Psammophis*.

A group of 120 species (87 lizards, 31 snakes, 2 turtles) were found to have FMRs in the range 81-90, that is, with males substantially larger than females. In this group, 60 were iguanids in 10 genera, but *Anolis* was by far the best represented, with 33 species. Other lizards were geckonids (2 genera), agamids (1 genus), teiids (4 genera), lacertids (3 genera) and skinks (3 genera). The 31 snakes belonged to 13 genera of colubrids, elapids and crotalids; *Crotalus* with 13 species and *Lampropeltis* with 4 species were the best represented.

At the upper end of the scale, with FMRs exceeding 130, that is with females very large, are 37 species of snakes

and 20 turtles (Fig. 5). All the turtles are emydids and trionychids. Species of the genera *Graptemys* and *Trionyx* were found to have FMRs much higher than in any other reptils. The snakes include a boid, 2 typhlopids, 17 natricines, 4 alsophiines, 7 other miscellaneous colubrids, 2 oxyuranines and 2 crotalids.

The group with somewhat smaller FMRs, in the range 121 to 130, was found to include 30 snakes and only 2 lizards, the latter both rainforest iguanids, *Anolis vittigerus* and *Polychirus marmoratus*. The snakes included a boid, a typhlopid, a viperid, 2 oxyuranines, 12 natricines, 4 dipsadines, and 9 other miscellaneous colubrids. In the FMR range 111 to 120 were found 26 species of lizards of eight families, *Ablepharus* (2), *Anolis*, *Chamaeleo*, *Coleonyx*, *Gambelia*, *Ichnotropis*, *Lacerta* (2), *Lipinia*, *Mabuya* (3), *Moloch*, *Ophiomorus* (2), *Phyllodac-*

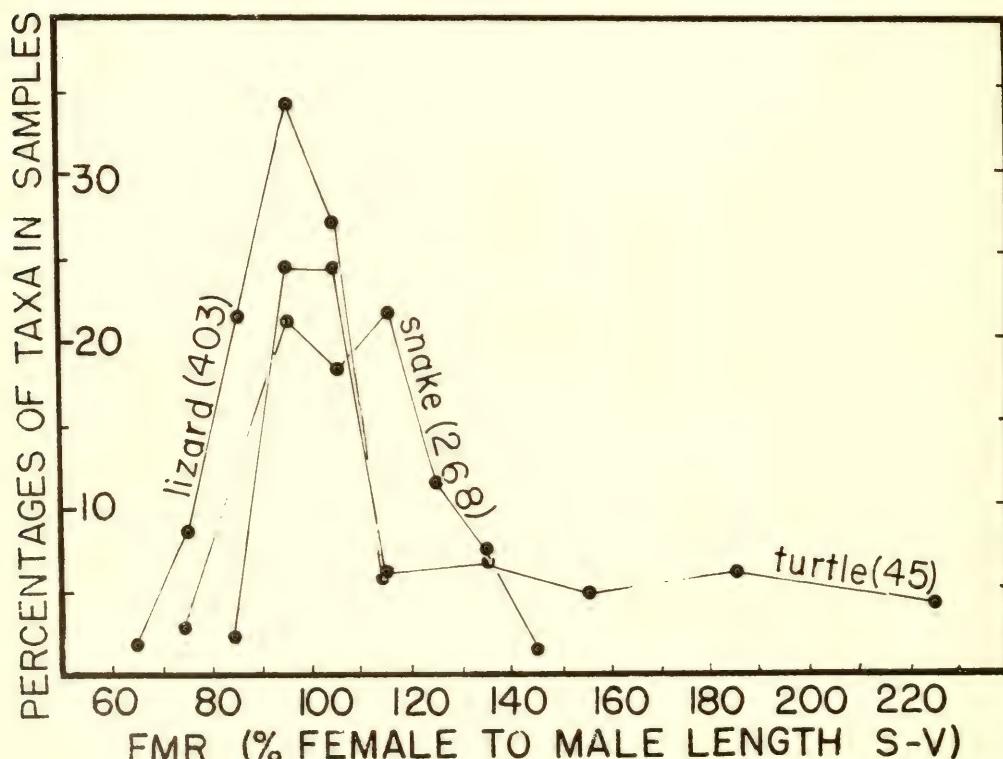


FIG. 5. Comparison of FMR in turtles, lizards and snakes. Each group has a wide range of FMR but trends differ with turtles attaining much higher ratios than squamates, and snakes attaining much higher ratios than lizards.

*tylus*, *Ptychodactylus*, *Sceloporus* (4), *Sphaerodactylus* (2), *Tropidurus*, *Xantusia*, and 63 other species of snakes of 42 genera.

More than half of the reptile taxa studied had FMRs in the range 91 to 110, that is with small or moderate size difference between the sexes, but only about 3.2 percent of the total 770 lacked SSD. Regardless of which sex is larger, the lizards and turtles in this range usually have male rivalry and combat. In the snakes, on the contrary, combat is known to occur mostly in those kinds having males definitely larger than females.

Significant trends in the correlation of FMRs with other specific traits are discernible in a few instances. Other such correlations are suspected but are still not demonstrable. In general, relatively large female size is demonstrably correlated with: (1) viviparous (vs. oviparous) reproduction, (2) large (vs. small) mean number of offspring in clutch or litter, (3) temperate (vs. tropical) climate where the species occurs, and (4) small (vs. large) body size. All these factors are interrelated. There are many species that are exceptions to the general trends.

According to Trivers' (1972) theory, intrasexual competition is closely linked with parental investment. Whichever sex (usually the female) devotes the most energy, risk and sacrifice to the offspring will be in short supply, and will be the object of competition by the opposite sex. Intrasexual competition will select for size, strength and aggressiveness, and the most successful competitors will have many mates and disproportionately large numbers of offspring.

Figure 6 demonstrates the trend from few eggs or young per clutch or litter in species having relatively small females to much larger broods in those species having relatively large females. Anoles and geckos make up a high proportion of the small-brooded species in this particular sample, whereas many of the large-brooded species are naticine

snakes. Striking exceptions to the general trends are seen in *Ctenosaura similis* and *Iguana iguana*, which have relatively small females, yet these produce large clutches, with more eggs than other lizards and more than most snakes.

Figure 7 demonstrates the trend in squamate reptiles from a low incidence of viviparity in those species having relatively small females to a high incidence of viviparity in those having relatively small males. Viviparous species are committed to a strategy of relatively long intervals between broods during gestation, compensated by moderate or large numbers of young per brood. As a container and carrier of the eggs and embryos, the female is subject to selective pressure to attain adequately large size.

Figure 8 demonstrates the related trend in squamates from a high percentage of tropical species among those with relatively large males to a minority of tropical species (i.e., mostly temperate zone species) among those with relatively large females. The most plausible explanation of this trend is that tropical species, having continuous breeding in some instances, or at least having an extended breeding season, are under less selective pressure to increase their size as egg containers than are those more restricted to a short and concentrated breeding season in the temperate zone.

Figure 9 shows mean sexual size ratios in lizards and snakes of various body-size groups. The main trend seems to be from larger mean size in the groups of species having relatively large males to smaller mean size in the groups of species having relatively large females. However, some points on the graph deviate from the general trend. Also each FMR grouping includes species over a wide size-range, and the correlation between FMR and body size is not statistically significant.

Both Ralls (1976) and Kolata (1977) after examining the evidence, mainly in mammals and birds, concluded that no one of the current theories could satis-

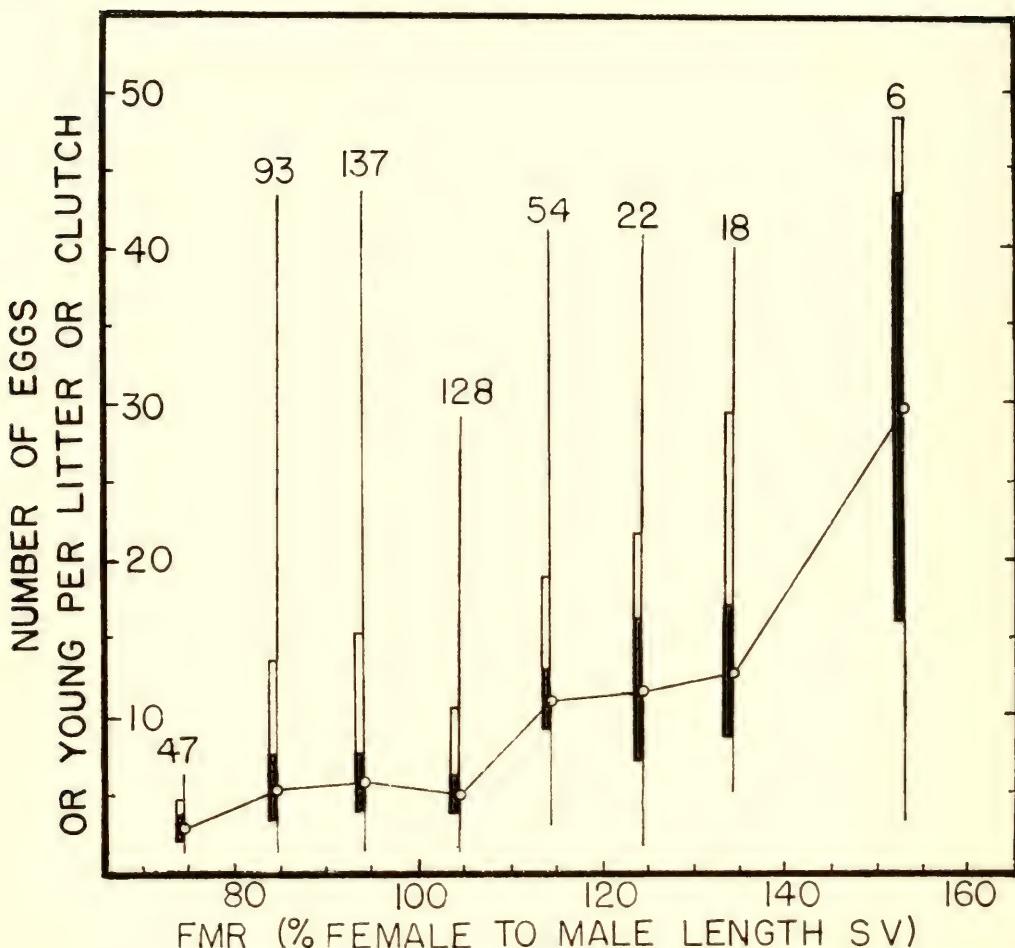


FIG. 6. Correlation of mean number of offspring per brood with FMR in 505 taxa of squamate reptiles showing trend from few young in kinds having relatively large males to many young in kinds having relatively large females. For each sample, mean, range, standard deviation, and two standard errors on each side of the mean are shown. Major sources of information on brood size were: Fitch 1970, Kopstein 1941, Pope 1935, and Wright and Wright 1957, but many others also were utilized. For some of the taxa that were included, only one record of a brood was available.

factorily explain all instances in which sexual size differences exist as each case is somewhat different, and the important effects of ecological and physiological factors have to be taken into account. The records herewith accumulated for reptiles certainly support the supposition that the sources of sexual size differences are complex and varied.

Freshwater turtles have progressed farthest in evolving disparate sizes in the sexes, with females commonly 1.4 to 1.8 times the linear dimensions of

males and 3 to 6 times their bulk (*Deirochelys*, *Graptemys*, *Pseudemys*, *Chrysemys* and *Trionyx*). In all of these, time to maturity is accelerated in males as compared with females. Usually the male's development from hatching to sexual maturity occurs in from 50 to 60 percent of the time required by the female. The result should be an excess of males, and the production of females so large and bulky that they are relatively safe from natural enemies and are able to utilize certain food resources

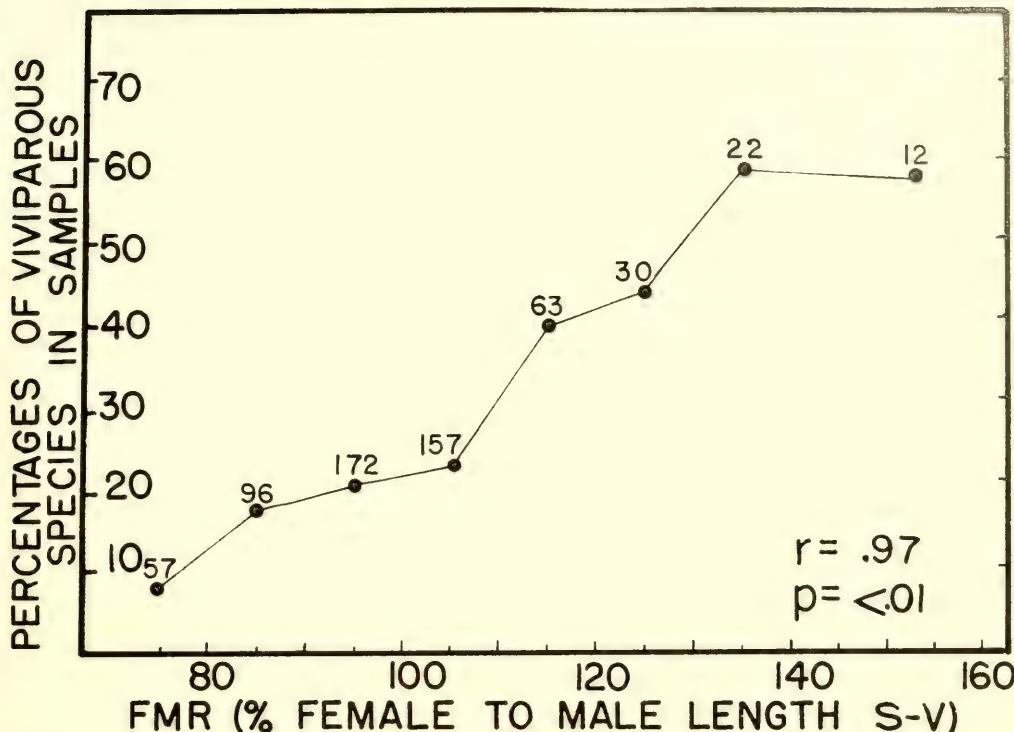


FIG. 7. Correlation of oviparity with relatively large male size vs viviparity with relatively large female size in 609 species of squamate reptiles.

not available to the males. Sex ratios of several of these species approximated 1:1 in field samples (Bury, 1979). In a recent study of *Graptemys geographica* at Lake of Two Mountains, Quebec, Gordon and MacCulloch (1979) found the population to be biased in favor of males. On the contrary, Seigel (1979) found that in a population of *Malaclemys terrapin* in Brevard County, Florida, females outnumber males by as much as 5 to 1.

Bull and Vogt (1979) found that in *Graptemys*, sex is controlled by environmental temperature during the middle third of the incubation period. Clutches kept at 25°C in the laboratory produced nearly all male hatchlings, whereas clutches kept at 30.5° produced almost all females. Natural nests that were monitored likewise produced biased sex ratios in hatchlings, depending whether the site was warm and sunny (females predominant) or cool and shaded (males predominant).

Regardless of which sex is the larger, SSD relieves intraspecific competition by partitioning food resources. Anoles are typical of reptiles having relatively large males, and for this genus Schoener (1967) and others have amply demonstrated that males, on the average, take larger food items often of different taxa from those taken by females. Also, in anoles the sexes may occupy somewhat different habitat niches; in species having tree-trunk to ground orientation, males usually perch higher.

At the opposite end of the scale, in species with relatively large females, reproductive success is promoted by the fact that reproductive females are relieved from competition by immatures as well as by males. In a study of Kansas *Thamnophis sirtalis* (FMR 123), I found incomplete partitioning of food resources which may be typical of snakes having SSD in this range. Average weight of females was 155 per cent of male

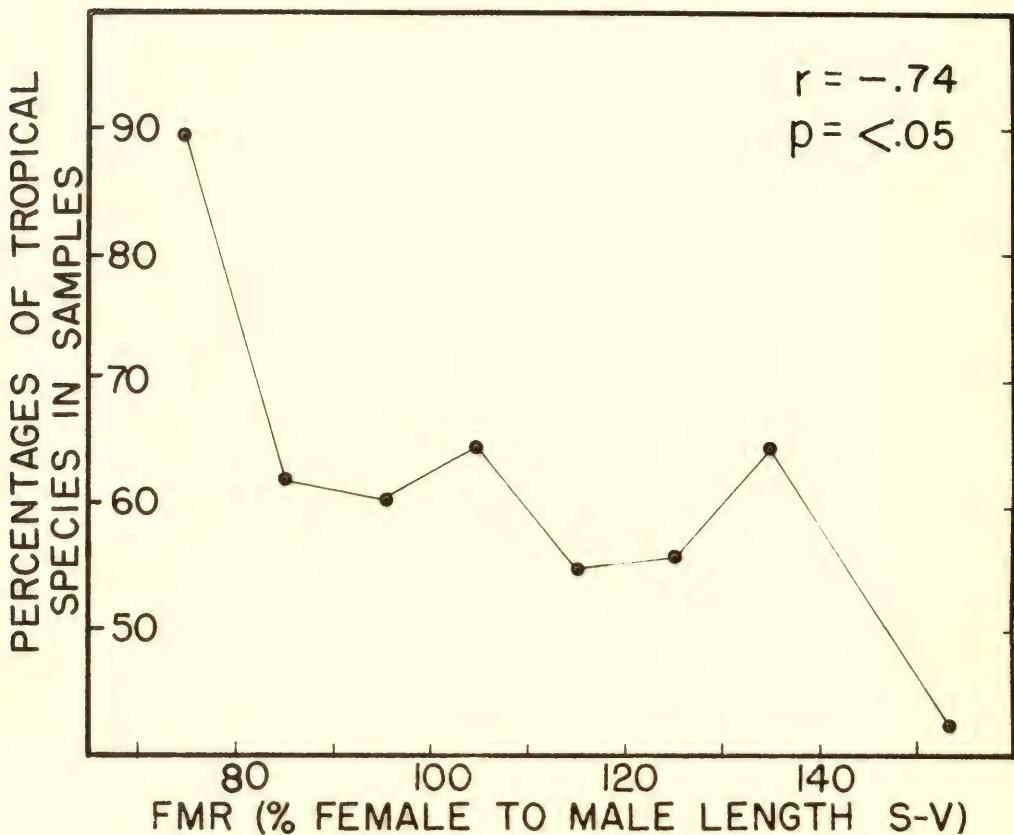


FIG. 8. Correlation between SSD and climate in squamate reptiles; a trend is evident, with a high percentage of species having relatively large males in tropical climates, and a high percentage having relatively large females in temperate-zone climates.

weight and females took larger food objects, especially mammals. Voles (*Microtus ochrogaster*) and wood mice (*Peromyscus leucopus*) were found to be the mainstay of the female diet, but both of these abundant small rodents are beyond the capacity of most males, which prey chiefly upon frogs. On the same area incomplete partitioning of food resources was found in *Coluber constrictor* (FMR 110). The large females were found to take voles and mice more often than did males, which tended to be more arboreal and had a higher component of insect prey.

*Graptemys pulchra* provides the most extreme case of SSD with the female averaging more than 15 times the male's bulk, and requiring 3 to 4 times as long

to attain sexual maturity. Sexual dimorphism is correlated with food habits, the adult female being specialized for mollusk-eating, with powerful jaws adapted for crushing shells, whereas the male, a more typical emydid in appearance, feeds to a large extent on soft-bodied insects (Ernst and Barbour, 1972).

Reptiles have not evolved such extreme SSD as some other groups of animals. The deep sea ceratioid angler fishes for instance have carried reduction of male size much further; the diminutive males attach permanently to the female and derive sustenance from her in a relationship that has been described as sexual parasitism (Bertelsen, 1951). The tiny males of some argiopid spiders which live like commensals in the webs

of their much larger mates, provide examples of another type of dependence

on the female, leading to extreme reduction in male size (Gertsch, 1949).

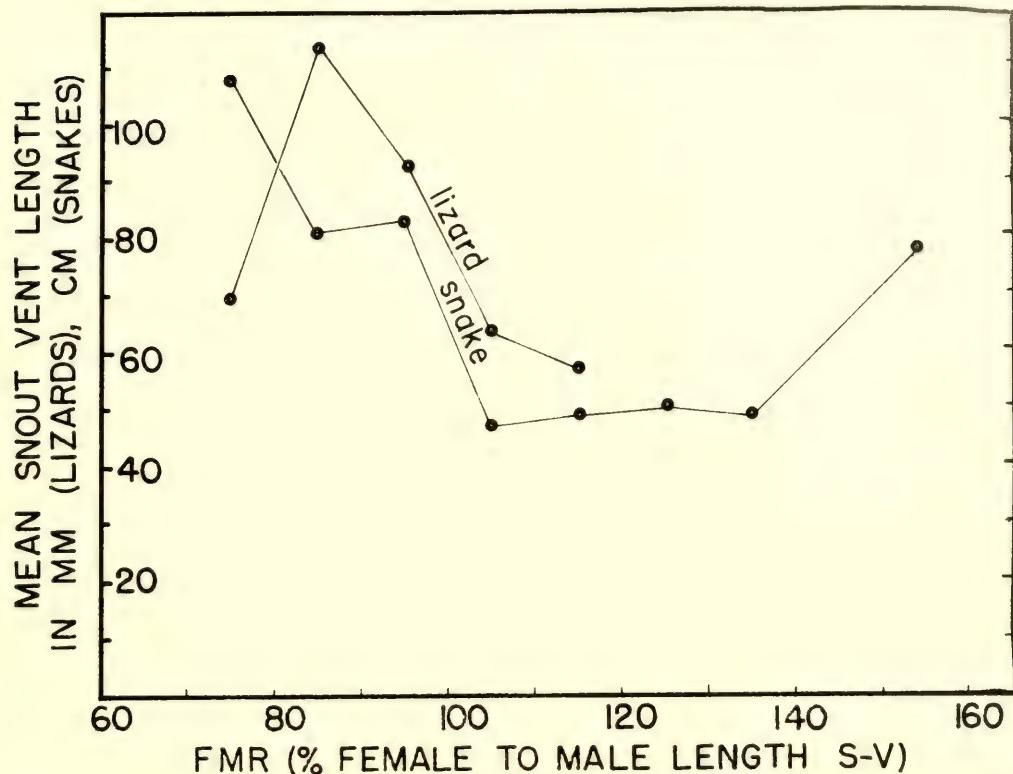


FIG. 9. Average adult size in lizards and snakes correlated with SSD showing that in both groups SSD (especially with male superiority) tends to be greater in species of large body size and less in small species.

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## APPENDIX I

Alphabetical list of reptiles, with female-to-male percentages,  
snout-vent lengths

Following each FMR figure, where available, are the male average and (in parentheses) the range and the number in the sample series; the same figures for females follow, and finally the source, abbreviated to the initials of the author(s) with the year of publication. These sources correspond with the publications listed in the Literature Cited in most instances. However, the abbreviation HSF<sup>a</sup> indicates figures from my own unpublished field data or museum specimens examined. The abbreviation var for "various sources" is used in instances where data are based on two or more publications.

- Ablepharus kitaibelii* 115 39.7(33-47) 45.7(35-51) IEF & SV 61.  
*Ablepharus wahlbergii* 110.6 42.0(38-46 in 4) 46.5(44-52 in 4) var.  
*Acanthodactylus cantoris* 87 54(39-85 in 17) 47(36-58 in 14) SCA 63.  
*Acanthophis antarcticus* 131 440(320-670 in 73) 578(375-825 in 50) RS 80C.  
*Achalinus spinalis* 125.4 265.6(217-340 in 5) 332.4(320-368 in 5) var.  
*Agama agama* 86.4 (99-123 in 7) (80-112 in 7) var.  
*Agama agilis* 87.4 87.3(79-94 in 26) 76.2(64-89 in 20) SCA 63.  
*Agama atricollis* 89.3 153.2(134-171 in 5) 137.7(118-153 in 4) var.  
*Agama hispida* 95.2 103.3(82-134 in 10) 98.5 (82-118 in 8) var.  
*Agama pallida* 109.3 61.2(55-67 in 20) 67.0 (59-81 in 20) YLW 71.  
*Agama tuberculata* 93 121(100-140 in 96) 113 (96-138 in 149) RCW 78.  
*Agkistrodon contortrix* 93.5 627.9(501-890 in 116) 586.9(500-678 in 98) HSF<sup>a</sup>.  
*Agkistrodon halys* 112 664.2(480-784 in 9) 743 (697-840 in 4) KK 38.  
*Agkistrodon piscivorus* 96 565(450-900 in 96) 493(450-800 in 90) RDB 66.  
*Ahaetulla prasina* 121.5 792(710-874 in 5) 962 (773-1075 in 12) FK 41.  
*Alligator mississippiensis* 73 3500 2550 (total lengths) RHC & TJ 79.  
*Alopoglossus atriventris* 105.9 41-46 43-49 JRD & PS 75.  
*Alopoglossus copi* 111.1 51.2(44-51 in 5) 57.0 (48-62 in 7) WED ms.  
*Amblyodipsas unicolor* 149.5 431(366-495 in 4) 702(410-705 in 4) var.  
*Amblyrhynchus cristatus* 85 341 290 JBI 79.  
*Ameiva ameiva* 95 114(90-142 in 110) 105 (90-125 in 78) WED ms.  
*Ameiva auberi* 82.6 93(78-136 in 23) 77(60-115 in 23) AS 70.  
*Ameiva festiva* 86.1 104.1(94-115 in 16) 89.6 (78-104 in 27) HSF<sup>a</sup>.  
*Ameiva quadrilineata* 96.6 72.5(66-79) 70.0 (62-78) HFH 63.  
*Ameiva undulata* 83.8 103.6(93-115 in 43) 86.9(78-106 in 74) HSF<sup>a</sup>.  
*Amphibolurus maculosus* 91 67 61 FJM 73.  
*Amphiesma sauteri* 115.5 260(237-282 in 8) 300.5(261-333 in 10) EVM 62.  
*Amphiesma stolata* 133 411(400-429 in 11) 587.4(478-654 in 10) FW 11.  
*Amphisbaena alba* 103.1 433(305-537 in 34) 447(353-655 in 43) PEV 55.  
*Amphisbaena fuliginosa* 97 (251-397) (224-402) in 17 JRD & PS 75.  
*Anniella geronimensis* 94 120.2(111-134 in 20) 113.0(111-129 in 18) HSF<sup>a</sup>.  
*Anniella pulchra* 102 129.2(119-142 in 13) 123.0(110-132 in 9) HSF<sup>a</sup>.  
*Anolis aeneus* 71 69.2(67-72 in 10) 49.3(48-52 in 10) TS & AS 71A.  
*Anolis allisoni* 74 82.6 in 70 61.0 in 43 TWS 70.  
*Anolis allegus* 75.4 56.7 in 202 42.7 in 97 TWS 70.  
*Anolis alutaceus* 92.0 35.8 in 55 32.8 in 70 TWS 70.  
*Anolis angusticeps* 88 42.0 in 26 37.0 in 37 TWS 70.  
*Anolis aquaticus* 88.7 65.9(57-71 in 10) 58.6 (59-62 in 9) HSF 76.  
*Anolis argillaceus* 81 44.3 35.8 TWS 70.  
*Anolis attenuatus* 95 84.5(78-95 in 24) 80.6 (74-90 in 18) HSF 76.  
*Anolis auratus* 104.4 44.6(40-49 in 31) 46.6 (43-49 in 8) HSF 76.  
*Anolis auratus sinaloae* 104 43.9(39-48 in 14) 45.9(42-50 in 11) MSH 73.  
*Anolis bimaculatus* 71 85.5 60.5 EEW 74.  
*Anolis biporcatus* 102 87.0(73-98 in 24) 88.7 (77-97 in 19) HSF 76.  
*Anolis biseutiger* 106 37.3(33-43 in 42) 39.4 (36-44 in 33) HSF 76.  
*Anolis bombiceps* 110 55-71 65-74 JRD & PS 75.  
*Anolis bourgai* 103.1 54.6(47-61 in 24) 56.3 (46-65 in 13) HSF 76.

- Anolis bremeri* 70 65.3(58-72 in 9) 45.6(39-52 in 9) OHG 72.
- Anolis brevirostris* 89 47.0 in 79 42.0 in 28 TWS 70.
- Anolis capito* 106.4 84.2(78-90 in 13) 89.6 (83-96 in 13) HSF 76.
- Anolis carolinensis* 79 59.9(54-66 in 14) 47.3 (41-53 in 12) HSF 76.
- Anolis carpenteri* 105 38.5(35-41 in 6) 40.4 (35-41 in 14) HSF 76.
- Anolis chlorocyanus* 76 71.4 in 184 54.0 in 90 TWS 70.
- Anolis christophei* 92 47.6 43.7 TS 70.
- Anolis chrysolepis* 105 71.5(66-79 in 29) 74.4 (67-80 in 32) HSF 76.
- Anolis coelestinus* 78.3 68.6 in 414 53.6 in 174 TWS 70.
- Anolis concolor* 74 68.3(60-80 in 70) 50.5(45-60 in 44) MJC & PLD 73.
- Anolis cooki* 70 59.5 41.6 TWS & AS 71B.
- Anolis crassulus* 88 48.3(39-53 in 8) 42.7(35-56 in 7) HSF 76.
- Anolis cristatellus* 79 63.6 in 327 44.6 in 204 TWS 70.
- Anolis cupreus* 88 47.4(41-53 in 233) 41.7(37-48 in 239) HSF 76.
- Anolis cupreus hoffmanni* 97 44.1(38-52 in 314) 42.6(38-51 in 166) HSF 76.
- Anolis cupreus macrophallus* 82 49.6(43-54 in 53) 40.8(34-46 in 33) HSF 76.
- Anolis cupreus spilomelas* 84 49.6(41-55 in 57) 41.7(36-49 in 23) HSF 76.
- Anolis cuprinus* 73 63.3(58-69 in 22) 46.5(42-53 in 15) HSF 76.
- Anolis cuvieri* 92 41.7 in 22 38.4 in 13 TWS 70.
- Anolis cybotes* 77 65.3 in 230 50.2 in 133 TWS 70.
- Anolis damalus* 110 43.1(37-48 in 9) 47.5(41-52 in 12) HSF 76.
- Anolis distichus* 87 50.2 in 450 43.2 in 262 WED & AS 58.
- Anolis distichus biminiensis* 90 46.7(38.3-49.8 in 10) 41.8(36.3-44.2 in 4) JAO 48.
- Anolis dollfusianus* 94 39.0(35-43 in 54) 36.7 (32-40 in 42) HSF 76.
- Anolis equestris* 93 170.9 in 95 158.4 in 66 TWS 70.
- Anolis evermanni* 74 70.7 52.4 TWS & AS 71B.
- Anolis frenatus* 82 132.4(121-143 in 15) 108.9 (100-118 in 20) HSF 76.
- Anolis fuscoauratus* 108 42.0(39-43 in 12) 45.3 (40-50 in 12) HSF 76.
- Anolis fuscoauratus kugleri* 102 44.5(40-49 in 9) 45.3(41-48 in 10) MSH 73.
- Anolis gadovii* 89 70.6(62-76 in 10) 62.6(56-69 in 12) HSF 76.
- Anolis garmani* 75 110 82.5 TWS 70.
- Anolis gemmosus* 94 62.5(58-66 in 38) 58.5 (56-63 in 28) HSF 76.
- Anolis grahami* 68 65.5 44.0 TWS & AS 71A.
- Anolis grahami aquarum* 73 61.8 45.1 TWS & AS 71A.
- Anolis gundlachi* 69 64.8 45.2 TWS & AS 71B.
- Anolis hendersoni* 84 47.9 in 165 40.2 in 86 TWS 70.
- Anolis heteropholidotus* 109 48.6(45-51 in 10) 53.1(49-58 in 7) HSF 76.
- Anolis homolechis* 78 52.3 in 355 40.7 in 107 TWS 70.
- Anolis humilis* 105 36.7(32-43 in 155) 38.5 (34-43 in 106) HSF 76.
- Anolis intermedius* 99 46.0(39-54 in 241) 45.5 (39-53 in 98) HSF 76.
- Anolis isthmicus* 89 54.4(50-63 in 25) 48.4 (44-58 in 9) HSF°.
- Anolis kemptoni* 104 48.0(45-53 in 13) 50.1 (46-54 in 21) HSF 76.
- Anolis krugi* 79.4 49.7 39.3 TWS & AS 71B.
- Anolis lemurinus* 104 67.0(59-79 in 13) 69.6 (59-78 in 16) HSF 76.
- Anolis limifrons* (Costa Rica) 103 37.5(33-43 in 392) 38.6(34-45 in 276) HSF 76.
- Anolis limifrons* (Panama) 99 43.9(38-48 in 8) 43.25(41-46 in 8) HSF 76.
- Anolis lineatopus* 69 60(50-70) 42(37-47) TAJ 73.
- Anolis lionotus* 84.8 71.5(65-78 in 19) 60.6 (56-68 in 24) HSF 76.
- Anolis loysiana* 89 40.4 in 18 36.0 in 7 TWS 70.
- Anolis lucius* 84 63.3 in 156 53.2 in 108 TWS 70.
- Anolis megapholidotus* 98 45.6(41-53 in 28) 44.6(41-49 in 14) HSF 76.
- Anolis nebulosus* 100 42.0(35-49 in 58) 42.0 (35-49 in 44) HSF 76.
- Anolis nigrolineatus* 94 50.9(47-55 in 14) 48.0 (45-51 in 15) HSF 76.
- Anolis occultus* 100 39.0 39.2 TWS & AS 71B.
- Anolis olssoni* 91 44.8 in 91 40.6 in 84 TWS 70.
- Anolis opalinus* 82 49.5 40.5 TWS & AS 71A.
- Anolis ortoni* 96 46.8(43-54 in 9) 44.8(42-48 in 8) HSF 76.
- Anolis pachypus* 101 45.5(40-50 in 32) 46.0 (41-50 in 24) HSF 76.
- Anolis pentaprion* 81 74.2(70-79 in 5) 60.0 (57-63 in 5) HSF 76.
- Anolis peraccae* 93 49.9(46-52 in 21) 46.3(44-48 in 9) HSF 76.
- Anolis pinchotti* 90 46.2(40-52 in 95) 41.5(38-46 in 59) MJC & PLD 73.
- Anolis poecilopus* 96 63.5(56-72 in 8) 61.0 (56-68 in 9) HSF 76.
- Anolis polylepis* 93 50.9(45-57 in 40) 47.3(41-53 in 48) HSF 76.
- Anolis poncensis* 87 45.6 39.6 TWS & AS 71B.
- Anolis porcatus* 72 71.2 in 114 51.5 in 62 TWS 70.
- Anolis pulchellus* 80 46.1 in 108 37.0 in 24 TWS 70.
- Anolis punctatus* 88 80.5(79-83 in 4) 71.5(64-77 in 12) HSF 76.
- Anolis punctatus boulengeri* 103 65-80 66-75 JRD & PS 75.

- Anolis quercurorum* 89 40.1(37-46 in 26) 35.8 (32-41 in 16) HSF<sup>o</sup>.
- Anolis richardi* 81 68.3(65-74 in 10) 66.6(65-69.8 in 10) TS 70.
- Anolis rodriguezi* 101 43.3(40-46 in 15) 43.7 (40-49 in 23) HSF 76.
- Anolis roquet* 77 74(72-76 in 10) 56.9(53-62 in 10) TS 70.
- Anolis sagrei* 73 54.5 in 192 39.7 in 62 HSF 76.
- Anolis sagrei stejnegeri* 79 53.9(49-60 in 20) 42.4(40-44 in 20) WED & AS 58.
- Anolis semilineatus* 86 40.7 in 57 35.2 in 34 TWS 70.
- Anolis sericeus* 90 45.4(40-52 in 47) 41.0(36-47 in 34) HSF 76.
- Anolis subocularis* 76 51.0(44-63 in 49) 38.8 (33-48 in 19) HSF 76.
- Anolis stratulus* 86 46.7 in 63 39.9 in 7 TWS & AS 71B.
- Anolis taylori* 79 71.8(64-78 in 45) 57.0(53-64 in 21) HSF 76.
- Anolis trachyderma* 115 44.4(38-52 in 129) 51.2(46-57 in 101) HSF 76.
- Anolis tropidogaster* 96 50.0(43-55 in 24) 48.0 (43-54 in 15) HSF 76.
- Anolis tropidolepis* 99 50.6(43-59 in 298) 50.1 (43-58 in 175) HSF 76.
- Anolis tropidonotus* 81 52.3(46-55 in 16) 42.4 (36-53 in 34) HSF 76.
- Anolis uniformis* 98.1 37.4(35-40 in 29) 36.7 (34-38 in 13) HSF 76.
- Anolis valencienni* 86.3 79.4 68.5 TWS & AS 71.
- Anolis villai* 89 51.5(43-60 in 64) 46.0(37-53 in 28) HSF & RWH 76.
- Anolis vittigerus* 125.4 52.3(45-57 in 7) 65.6 (60-70 in 7) HSF 76.
- Anolis wattsi* 87 47.5 41.2 EEW 74.
- Anolis woodi* 86.6 80.8(78-87 in 4) 69.9(61-77 in 10) HSF 76.
- Aparallactus lunulatus* 131 284(261-315 in 4) 373(310-410 in 4) var.
- Aparallactus modestus* 120 386(377-402 in 4) 465(435-483 in 4) var.
- Aplopeltura boa* 102.5 499(413-546 in 6) 511 (455-582 in 11) FK 41.
- Aporosaura anchietae* 89.8 49 44 SRG & MDB 79.
- Arthrosaura kockii* 107 46.4(40-54 in 13) 49.5 (45-53 in 13) MSH 73.
- Arthrosaura reticulata* 86 57-66 45-61 JRD & PS 75.
- Atheris squamiger* 112.8 479(369-559 in 4) 540(416-598 in 5) var.
- Atractaspis bibroni* 110.8 512(370-575 in 6) 566.5(470-611 in 4) var.
- Atractaspis irregularis* 110 494(466-541 in 5) 543(510-621 in 5) var.
- Atractus carrioni* 142 216(135-280 in 5) 307 (260-350 in 5) JMS 60 (incl. juv.).
- Atractus elaps* 111 344.5(152-560 in 34) 382 (134-631 in 23) JMS 60 (incl. juv.).
- Atractus major* 111 326(120-852 in 32) 364 (140-852 in 24) JMS 60 (incl. juv.).
- Atractus multicinctus* 110 284(262-300) 314 (286-354) JMS 60 (incl. juv.).
- Atractus occipitoalbus* 126 189(93-269 in 7) 231(135-298 in 14) JMS 60 (incl. juv.).
- Atretium schistosum* 120 431 in 7 518 in 7 FW 12.
- Austrelaps superbus* 92.1 766 in 10 706 in 27 RS 77.
- Bachia flavescens (cophias)* 108 64.8(60-73 in 9) 70(58-80 in 15) MSH 73.
- Bachia flavescens (vermiforme)* 99 57-64 55-65 JRD & PS 75.
- Bachia trinasa* 104 65.5(56-72 in 11) 68.1(59-79 in 9) WED ms.
- Basiliscus basiliscus* 78 218 170 RWV 78.
- Basiliscus vittatus* 85.5 140.9(121-167 in 29) 120.5(110-131 in 17) HSF<sup>o</sup>.
- Bitis arietans* 93.1 865.6(762-1030 in 21) 806.6 (710-965 in 12) VFMF 30.
- Blanus cinereus* 100 210(197-254 in 12) 210 (194-235 in 18) JB & HStG 63.
- Boaedon lineatus* 140 629(443-801 in 4) 879 (618-1047 in 8) var.
- Boiga dendrophila* 96 1392(993-1607 in 4) 1332(1275-1395 in 6) FK 41.
- Boiga pulverulenta* 106 825(764-884 in 4) 874 (840-944 in 4) var.
- Bothrops atrox* 115.4 872.7(701-1200 in 59) 1007.4(706-1390 in 53) HSF<sup>o</sup>.
- Bothrops lansbergi* 101 357(255-476 in 33) 361(250-500 in 52) JR 79.
- Bothrops nasutus* 96.4 354.7(273-450 in 23) 337.1(270-450 in 17) JR 79.
- Bothrops pulcher* 153 353.6(333-374 in 4) 540.5(435-634 in 8) JR 79.
- Bothrops punctatus* 144 580(517-678 in 8) 833.7(550-1065 in 8) JR 79.
- Bothrops schlegelii* 111 420.8(304-557 in 11) 466.3(302-704 in 14) JR 79.
- Brachymeles gracilis* 93 (59.4-86) (57.2-78) WCB & DSR 67.
- Cacophis kreftii* 112.2 235 264 RS 80B.
- Cacophis harriettae* 124.6 286 357.6 RS 80B.
- Cacophis squamulosus* 129 390 in 48 502 in 61 RS 80B.
- Calamaria agamensis* 117.7 237(200-268 in 28) 279(245-326 in 27) FK 41.
- Calamaria gervaisi* 126 191(170-210 in 8) 254 (190-321 in 9) RFI & HM 65.
- Calamaria lumbricoidea* 115 413(384-485 in 26) 477(337-555 in 36) CPJH 41.
- Calamaria multiplicata* 126 218.1(183-260 in 159) 275.5(225-358 in 155) CPJH 41.
- Calamaria pavimentata* 116 238.2(193-286 in 5) 266.2(219-336 in 9) RFI & HM 65.
- Calamaria virgulata* 116.1 296(211-330 in 16) 343.7(275-390 in 10) FK 41.
- Callisaurus draconoides* 89 78.9(70-88 in 43) 70.2(63-80 in 46) ERP & WSP 72.

- Callisaurus draconoides rhodostictus** 89.7 68.8  
(31-89 in 13) 61.6(33-80 in 24) HSF°.
- Candoia carinata** 137 568.9(487-640 in 10)  
780(544-1089 in 23) SBM 79.
- Carphophis vermis** 116.7 244.1(216-288 in 90)  
285(208-325 in 73) HSF°.
- Causus lichtensteini** 115.2 464(376-574 in 4)  
537(442-660 in 4) var.
- Causus rhombeatus** 95 664.2(503-830 in 5)  
632(540-740 in 7) var.
- Cemophora coccinea** 79 832 650 AHW &  
AAW 57.
- Cerastes cerastes** 120 514.4(415-640 in 7)  
617.25(567-760 in 4) AEL & SCA 67.
- Cerberus rhynchos** 118 480.2(420-556 in 6)  
566.5(482-618 in 4) FK 41.
- Cercosaura ocellata** 103 50-65 54-63 in 52  
JRD & PS 75.
- Chamaeleo bitaeniatus** 101 116(74-108 in 4)  
117.3(79-97 in 4) var.
- Chamaeleo dilepis** 107 131.3(71-172 in 10)  
140(97-164 in 9) var.
- Chamaeleo etiennei** 109 79.3(68-97 in 8) 86.4  
(65-115 in 15) var.
- Chamaeleo namaquensis** 106 112.6(75-158 in  
30) 119.6(88-140 in 50) BRB 73.
- Chamaeleo pumilis** 107.1 73.5(53-93 in 65)  
78.8(51-102 in 86) BRB 73.
- Chamaeleo quilensis** 120 94(86-111 in 19)  
112.5(89-127 in 11) RFL 64.
- Chamaeleolis chamaeleonides** 99 161.7 in 12  
160.5 in 33 TS 70.
- Charina bottae** 112.2 499 561 RAN & RFH 74.
- Charina bottae utahensis** 122.2 444 543 RAN  
& RFH 74.
- Chelonia mydas** 106.2 904(710-1040) 960(787-  
1143) CHE & PWB 72.
- Chelydra serpentina** 100 254(191-355 in 18)  
255(211-259 in 9) JLC & RRB 79.
- Chrysemys picta** 139 114(116-220 in 15) 158.1  
(130-155 in 30) JWG 67.
- Chrysopelia paradisi** 124 573(470-700 in 8)  
770(480-910 in 5) RM 68.
- Clelia rustica** 96.7 706(520-950 in 7) 681(450-  
875 in 9) FA 73.
- Clemmys guttata** 100 80 in 10 80 in 10  
RBB 79.
- Clemmys marmorata** 100 100-120 100-120  
RBB 79.
- Clemmys muhlenbergii** 107 67.0(61.8-89.7 in  
76) 71.7(67.9-86.9 in 74) CE 77.
- Clonophis kirtlandi** 110 525-675 550-775  
AHW & AAW 57.
- Cnemidophorus bacatus** 91.6 78.3 in 6 71.7  
in 6 JMW & TPM 69.
- Cnemidophorus calidipes** 91.4 73.8(70-79 in  
25) 67.2(66-68 in 6) WED 60.
- Cnemidophorus deppei** 92.8 73.2(60-92 in 182)  
67.9(60-81 in 260) HSF°.
- Cnemidophorus guttatus** 93 106(89-128 in 12)  
98(83-112 in 8) HSF°.
- Cnemidophorus hyperythrus** 97.4 61.4(55-72 in  
97) 59.7(53-70 in 116) DLB 66.
- Cnemidophorus inornatus** 103.5 56.0(50.5-65)  
58(47-66) PAM 67.
- Cnemidophorus lemniscatus** 79.4 76.7(60-97 in  
201) 60.9(50-78 in 194) JRL & LJC 73.
- Cnemidophorus lineatissimus** 89.4 91.5(78-105  
in 28) 81.7(75-90 in 14) JMW 70.
- Cnemidophorus parvusocius** 91.1 64.8(52-79 in  
274) 59.0(50-69 in 172) TPM & JMW 73.
- Cnemidophorus sacki** 93.3 70.7(55-58) 66(45-  
95) WWM 61.
- Cnemidophorus sexlineatus** 100.8 72.7(65-81 in  
88) 73.3(65-83 in 96) HSF°.
- Cnemidophorus tigris** 93.7 83.5(70-95 in 44)  
78.1(70-87 in 75) HSF°.
- Coleodactylus amazonicus** 105 21.2(20-23 in  
18) 22.3(18-24 in 17) MSH 73.
- Coleonyx variegatus** 106.8 58.4(53-65 in 55)  
62.3(56-70 in 23) WSP 72.
- Coleonyx variegatus utahensis** 113.9 54.1(37-66  
in 16) 61.6(44-70 in 12) WWT & BHB 66.
- Coluber constrictor** 110 721(513-1110 in 181)  
795(538-1210 in 177) HSF°.
- Coluber jugularis** 71.1 1496.6(1160-1840)  
1065.8(500-1272) IEF & SV 61.
- Coluber spinalis** 126 501(375-572 in 9) 631.2  
(483-755 in 7) CHIP 35.
- Coluber viridiflavus** 86.3 800.1(685-873 in 7)  
690.1(633-790 in 6) SB 68.
- Coluber viridiflavus xanthurus** 77 1208.5(740-  
1365 in 10) 930.4(865-1085 in 10) SB 70.
- Coniophanes fissidens** 113.6 263(225-335 in 15)  
298.8(230-425 in 27) GRZ, SBH & SS 79.
- Conolophus subcristatus** 91.1 383(350-417 in 8)  
349(313-383 in 8) CCC 69.
- Coronella austriaca** 102 515(440-600 in 31) 526  
(440-600 in 27) IFS & TEP 77.
- Corythophanes cristatus** 109 98.6(79-117 in 5)  
107.2(80-120 in 9) HSF°.
- Cosymbotus platurus** 98.5 55.0(53.7-56.3 in  
122) 54.1(52.9-56.8 in 173) GC 62.
- Crocodylus niloticus** 85.2 3416(3073-3743 in  
14) 2911(2600-3192 in 50) (total length)  
HBC 61.
- Crotalus atrox** 90.6 963 in 87 873 in 56 LMK  
37.
- Crotalus cerastes** 103.3 537 in 53 555 in 42  
LMK 37.
- Crotalus durissus** 88 1512 in 10 1334 in 10  
LMK 37.
- Crotalus durissus terrificus** 97 754(450-965 in  
12) 731(405-1140 in 18) JR 79.
- Crotalus enyo** 92 796 in 10 736 in 10 LMK 37.
- Crotalus horridus** 94 1073 in 10 1010 in 10  
LMK 37.
- Crotalus lepidus** 82.4 596(545-648 in 4) 492  
(445-540 in 4) AHW & AAW 57.
- Crotalus lepidus klauberi** 84.6 528 in 37 447  
in 32 LMK 37.
- Crotalus lucasensis** 87.1 1055 in 162 919 in  
110 LMK 37.
- Crotalus mitchelli** 93.6 842 in 49 788 in 27  
LMK 37.

- Crotalus mitchelli pyrrhus* 78 1092 in 10 847  
in 10 LMK 37.
- Crotalus mitchelli stephensi* 88 840 in 10 740  
in 10 LMK 37.
- Crotalus molossus* 90.5 967 in 37 875 in 23  
LMK 37.
- Crotalus molossus nigrescens* 84 1156 in 10  
969 in 19 LMK 37.
- Crotalus pricei* 82 562 in 10 460 in 10  
LMK 37.
- Crotalus ruber* 84 1285 in 10 1075 in 10  
LMK 37.
- Crotalus scutulatus* 87.9 858 in 121 754 in 48  
LMK 37.
- Crotalus tigris* 82 767 in 10 632 in 10 LMK 37.
- Crotalus triseriatus* 90 555 in 10 499 in 10  
LMK 37.
- Crotalus viridis* 91.5 753 in 274 682 in 222  
MK 37.
- Crotalus viridis concolor* 88 601 in 10 526 in  
10 LMK 37.
- Crotalus viridis helleri* 79.5 1102-1300 in 10  
860-1052 in 10 AHW & AAW 57.
- Crotalus viridis lutosus* 89.7 875 in 96 784 in  
48 LMK 37.
- Crotalus viridis nuntius* 78 688 in 10 537 in 10  
LMK 37.
- Crotalus viridis oreganus* 86.7 691 in 127 599  
in 83 LMK 37.
- Crotaphopeltis hotamboeia* 105 527(370-636 in  
14) 563.6(435-710 in 11) var.
- Crotaphytus collaris* 92.7 100.9(95-109 in 24)  
93.6(78-112 in 56) HSF<sup>a</sup>.
- Cryptoblepharus boutoni* 102 44(41.5-46.5 in  
30) 45(39.5-49.5 in 28) RM 31.
- Ctenosaura similis* 80 345(200-489 in 610) 276  
(200-347 in 283) HSF & RWH 78.
- Cyclura carinata* 81.6 276.3(191-360 in 47)  
225.4(190-292 in 45) JBI 79B.
- Cyclura cornuta* 92 534.5±3.88 468.0±10.87  
JBI 79B.
- Cyclura cychlura* 93.4 303 283 JBI 79B.
- Cyclura pinguis* 86 534.5 468.0 WMC 75.
- Cyrtodactylus malayanus* 109 98.9(82-107 in  
119) 107.7(97-117 in 36) RFI & BG 66.
- Cyrtodactylus pubisculus* 110.2 66.4(57-72 in  
54) 73.3(69-78 in 15) RFI & BG 66.
- Dasypeltis scabra* 117.1 564(425-710 in 8) 661  
(505-848 in 14) var.
- Deirochelys reticularia* 194 75-85 150-160  
RBB 70.
- Dendrelaphis picta* 114.3 500.3(445-594 in 8)  
572(435-646 in 24) FK 41.
- Diadophis punctatus* 111 249(215-312 in 227)  
279(221-368 in 408) HSF<sup>a</sup>.
- Dinodon flavozonatum* 82.6 883(790-1170 in 5)  
729.7(590-990 in 4) CHP 35; MAS 43.
- Dinodon orientale* 100 40-80 40-80 HF 65.
- Dinodon rufozonatum* 96.1 816.4(708-910 in 5)  
785.1(540-990 in 7) CHP 35; TPM 50.
- Dipsadoboa unicolor* 83.7 812.1(653-1093 in 5)  
680(635-725 in 4) var.
- Dipsas catesbyi* 96.3 395.9(260-520 in 99)  
381.2(270-580 in 105) HSF<sup>a</sup>.
- Dipsosaurus dorsalis* 95 127(115-145 in 377)  
120(110-142 in 200) JEM 71.
- Dispholidus typus* 102 1021.1(740-1290 in 8)  
1047(805-1293 in 9) var.
- Draco melanopogon* 105.6 79.5(67-87 in 343)  
84.0(77-90 in 83) RFI & BG 66.
- Draco quinquefasciatus* 101.5 96(87-107 in 248)  
97.4(86-107 in 62) RFI & BG 66.
- Drymoluber dichrous* 73.5 1041(802-1140 in  
11) 695.3(610-785 in 13) HSF<sup>a</sup>.
- Duberria lutrix* 118.2 263.7(164-355 in 8) 312.9  
(161-384 in 10) var.
- Echis carinata* 129 471-531 587-717 CRSP 74.
- Echis colorata* 97.7 642(551.5-728 in 20) 627  
(553-732.5 in 21) HM 65.
- Elaphe climacophora* 102 1325(1188-1720 in  
39) 1344(1210-1530 in 22) HF 78.
- Elaphe conspicillata* 100 900-1200 900-1200  
HF 65.
- Elaphe dione* 103 773.2(650-843 in 4) 794.3  
(720-885 in 4) CHP 35.
- Elaphe flavolineata* 103.7 1045(885-1178 in 5)  
1084(960-1198 in 8) FK 41.
- Elaphe longissima* 85.6 1126.6(835-1347) 963.7  
(665-1120) IEF & SV 61.
- Elaphe obsoleta* 96.0 1058(801-1530 in 256)  
1016(800-1372 in 168) HSF<sup>a</sup>.
- Elaphe porphyriaca* 100 701.2(678-733 in 6)  
700(651-742 in 5) CHP 35.
- Elaphe quadrivirgata* 92 900-1300 700-1200  
HF 65.
- Elaphe radiata* 107.9 1065(819-1267 in 13)  
1149(1018-1218 in 7) FK 41.
- Elapoides fuscus* 110 337(267-399 in 153) 371  
(308-434 in 155) FK 41.
- Emoia adspersa* 101.1 74.0(72-84 in 111) 74.9  
(70-81 in 21) TDS 79.
- Emoia atrocostata* 96.5 92.7(88-100 in 20)  
89.6(85-95 in 15) ACA & WCB 67.
- Emoia cyanura* 99.0 48.3(42-58 in 195) 47.7  
(41-56 in 82) TDS 80.
- Emoia lawesii* 101.7 98(90-106 in 16) 99.7  
(94-104 in 20) TDS 80.
- Emoia nigra* 94 108(93-120 in 107) 101.7(88-  
113 in 70) TDS 80.
- Emoia samoensis* 93.5 107(90-115 in 47) 100  
(89-113 in 37) TDS 80.
- Emydoidea blandingii* 95.1 215.5(182-234 in  
41) 204.2(179-218 in 33) TEG & TSD 79.
- Emys orbicularis* 106 149.6(142-163) 158.5  
(146-171) IEF & SV 61.
- Enhydrina schistosa* 111 782(800-858 in 4)  
847(890-950 in 4) HKV & BCJ 79.
- Enhydris enhydris* 109.3 397(333-446 in 16)  
434(378-513 in 18) FK 41.
- Enyaliosaurus clarki* 92.9 153 142 WED &  
ASD 59.
- Enyaliooides laticeps* 100 115(100-128 in 14)  
114.5(102-125 in 17) WED ms.
- Epicrates cenchria* 114 955(790-1257 in 13)

- 1089(975-1330 in 6) JWA, ECB & RD 65.  
*Eremias arguta* 93.4 59.7 55.8 IEF & SV 61.  
*Eremias guttulata* 99 48.0(39-53 in 7) 47.5  
 (38-57 in 6) SCA 63.  
*Eremias lugubris* 96 172(168-178 in 4) 165  
 (159-171 in 4) (total lengths) VFMF 30.  
*Eremias namaquensis* 90 160.8(145-184 in 14)  
 144.8(130-157 in 8) (total lengths) VFMF 30.  
*Eremias savagei* 97.7 41.9(33-48 in 29) 40.9  
 (35-50 in 27) RFL & CG 65.  
*Eretmochelys imbricata* 103.7 315.6(312-320)  
 327(255-360) RHM 65.  
*Eublepharis angramainyu* 88.8 142-154 in 8  
 126-137 in 5 SCA & AEL 66B.  
*Eumeces brevirostris* 103.6 62.2(60-69 in 4)  
 64.5(60-71 in 4) JRD 69.  
*Eumeces eggregius* 106 42.5(34-48 in 33) 45.1  
 (37-54 in 37) RHM 65.  
*Eumeces fasciatus* 98.8 72.7(66-82 in 120)  
 71.9(66-79 in 180) HSF°.  
*Eumeces gilberti* 90 91.3±1.4 in 59 82.4±1.1  
 in 31 TLR & HSF 47.  
*Eumeces gilberti cancellatus* 97 86.9±1.6 in 31  
 84.3±.92 in 35 TLR & HSF 47.  
*Eumeces gilberti placerensis* 95 89.6±.22 in 23  
 85.5±2.4 in 21 TLR & HSF 47.  
*Eumeces gilberti rubricaudatus* 102 86.5±1.17  
 in 40 88.1±1.35 in 18 TLR & HSF 47.  
*Eumeces inexppectatus* 97.9 66.8(55-77 in 11)  
 65.4(49-78 in 18) WED & AS 58.  
*Eumeces latiscutatus* 98.0 71.5(63.3-87.7 in 10)  
 70.0(58.8-81.3 in 11) TH 78.  
*Eumeces obsoletus* 101.8 111.9(100-128 in 146)  
 113.9(100-136 in 128) HSF°.  
*Eumeces ochoterenae* 102 48.3 49.4 JRD 69.  
*Eumeces septentrionalis* 101.1 78.6(71-85 in 5)  
 79.5(71-85 in 6) HSF°.  
*Eumeces skiltonianus* 101 62.7±.42 in 166  
 63.2±.48 in 134 TLR & HSF 47.  
*Eumeces skiltonianus utahensis* 103.6 63.7(60.1-  
 68.1 in 14) 66(62.0-70.5 in 19) WWT 57.  
  
*Farancia abacura* 165 600-1090 920-1875  
 AHW & AAW 57.  
*Farancia abacura reinwardti* 159 725-982 852-  
 1790 AHW & AAW 57.  
*Farancia erytrogramma* 148.5 622(270-870 in  
 17) 923(370-1340 in 27) JWG & JWC 77.  
*Ficimia olivacea* 95 367(251-483) 350(250-450)  
 LMH 75.  
*Ficimia quadrangularis* 95 212.1(87-304 in 74)  
 201.7(127-280 in 25) LMH 75.  
*Fordonia leucobalia* 119.2 383(337-511 in 6)  
 456.7(366-556 in 6) FK 41.  
  
*Gambelia wislizenii* 115.2 102(88-110 in 36)  
 117.5(112-132 in 25) WSP & ERP 76.  
*Gehyra australis* 103.8 63.4(59-68 in 5) 65.8  
 (63-70 in 5) RHB 64.  
*Gehyra oceanica* 97.0 79.4(74-90 in 14) 77.0  
 (74-86 in 18) TDS 80.  
*Gehyra variegata* 98.6 51.8(50-54 in 5) 51.0  
 (48-56 in 5) RHB 64.  
  
*Geochelone elephantopus ephippium* 82.1 2580  
 (2325-2950 in 25) 2120(1840-2700 in 61)  
 JVD 14.  
*Geochelone elephantopus vicina* 98.6 2690  
 (2400-3320 in 10) 2650(2125-3120 in 35)  
 JVD 14.  
*Geochelone radiata* 93.0 360 in 11 334 in 15  
 WA 78.  
*Geodipsas depressiceps* 116.1 296(230-360 in 4)  
 343.5(244-390 in 4) var.  
*Geophis brachycephalus* 116.9 339 394 FLD  
 67.  
*Geophis hoffmanni* 132 197 260 FLD 67.  
*Geophis nasalis* 104.5 285 298 FLD 67.  
*Geophis rhodogaster* 124 253 314 FLD 67.  
*Geophis semidoliatus* 128.9 290 374 FLD 67.  
*Gerrhonotus monticolus* 93.6 77.3(63-87 in 25)  
 72.4(63-85 in 24) HSF°.  
*Gerrhonotus moreleti* 92.5 88.6(81-94 in 6)  
 82.0(77-88 in 13) HSF°.  
*Gerrhonotus multicarinatus* 97.5 132.7(120-149)  
 in 22) 129.4(120-142 in 20) HSF°.  
*Gerrhonotus multicarinatus webbii* 98.2 132.8  
 (120-170 in 25) 130.5(120-152 in 22) HSF°.  
*Gonatodes albogularis* 100 40.1(36-45 in 23)  
 40.1(36-42 in 18) HSF°.  
*Gonatodes annularis* 101 47(40-50 in 6) 47.4  
 (39-55 in 7) MSH 73.  
*Gonatodes concinnatus* 99 42.4(32-52 in 8)  
 42.0(35-49 in 12) WED ms.  
*Gonatodes humeralis* 106 31-41 33-39 JRD &  
 PS 75.  
*Gongyloma baliodeira* 108 258.8(217-305 in  
 35) 278.5(245-314 in 36) CPJH 41.  
*Gopherus agassizii* 92.2 272(256-316 in 59)  
 251(231-301 in 32) AMW & RH 48.  
*Gopherus polyphemus* 106 230-341 238-368  
 RBB 79.  
*Graptemys barbouri* 195 (90-130) (150-230)  
 RBB 79.  
*Graptemys geographica* 196 115(93-136 in 45)  
 226(201-258 in 15) RCV 80.  
*Graptemys kohni* 181.9 (90-130) (150-250)  
 RBB 79.  
*Graptemys nigrinoda* 142.9 (75-100) (100-150)  
 RBB 79.  
*Graptemys ouachitensis* 167 123(109-137 in 68)  
 205(163-242 in 265) RCV 80.  
*Graptemys oculifera* 183.8 (75-110) (100-150)  
 RBB 79.  
*Graptemys pseudogeographica* 169 133(111-  
 151 in 68) 225(193-274 in 109) RCV 80.  
*Graptemys pulchra* 248 100(80-120) 248.5(212-  
 285) RMS 76.  
*Gyalopion canum* 106 211.9(116-292 in 39)  
 224.8(151-315 in 15) LMH 75.  
  
*Hemiaspis signata* 98.6 43.1 in 53 43.3 in 15  
 RS 77.  
*Hemidactylus frenatus* 96 53.5(52-54 in 179)  
 51.4(50-52 in 251) GC 62.  
*Hemidactylus mabouia* 105.6 59-67 in 6 61-72  
 in 4 GFW 53.

- Hemidactylus turcicus** 106.2 40.4±1.3 in 70  
43.0±1.5 in 51 JR & MP 71.
- Hemirhagerrhis nototaenia** 105.4 247.4(208-270  
in 5) 261(197-315 in 6) var.
- Heterodon nasicus** 116 385-550 430-660 DRP  
69.
- Heterodon platyrhinos** 107 400-1050 450-1200  
DRP 69.
- Heteronotia binoei** 107.8 41.7(34-49 in 91)  
45.0(39-49 in 27) RHB 68.
- Holarchus violaceus** 87.4 457.5(436-472 in 4)  
400(381-429 in 4) var.
- Holbrookia maculata** 107.6 48.9(43-60 in 31)  
52.6(42-63 in 70) HSF°.
- Holbrookia maculata approximans** 92.6 56.8  
(54-61 in 7) 52.0(50-55 in 9) WWM 61.
- Homalopsis buccata** 109 625(510-800 in 26)  
681(540-870 in 30) KG 70.
- Hydrophis torquatus** 97 813.6(705-918 in 4)  
786.4(732-940 in 4) EHT 65.
- Ichnotropis capensis** 95 55.0(38.3-66.7 in 56)  
52.3(40.6-61.7 in 52) RFL 64.
- Ichnotropis squamulosa** 94.9 220(208-235 in 8)  
208.3(190-223 in 11) (total lengths) VFMF  
30.
- Iguana iguana** 91 361(250-550 in 174) 327  
(236-411 in 169) HSF & RWH 77.
- Imantodes cenchria** 109 699.8(616-754 in 8)  
762.9(690-831 in 10) HSF°.
- Imantodes lentiferus** 105 616(471-682 in 11)  
645(534-710 in 4) WED ms.
- Iphisa elegans** 100 52.0(41-62) 52.2(46-60)  
JRD 64.
- Japalura swinhonis** 94.9 62.8(51-81 in 45) 60.3  
(50-74 in 34) YO 37.
- Kentropyx calcaratus** 97 105(92-115 in 28)  
102(94-116 in 24) WED ms.
- Kentropyx pelviceps** 96 75-115 in 29 80-111  
in 23 JRD & PS 75.
- Kentropyx striatus** 89 88.5(72-124 in 12) 79  
(72-94 in 17) MSH 73.
- Kerilia jerdoni** 103 512.6(362-854 in 7) 525.6  
(351-900 in 7) EHT 65.
- Kinosternum bauri** 101 89.1(78.3-103.9 in 6)  
89.8(74.1-110.7 in 15) WED & AS 58.
- Kinosternum bauri palmarum** 122 87.6(80.8-  
98.1) 107.6(101.6-119.0) WED & AS 58.
- Kinosternum flavescens** 97.5 103(80-115 in 23)  
100.5(73-117 in 21) YM 67.
- Kinosternum subrubrum** 118 78.3(71.1-88.7)  
92.5(75.5-106.9) JBI 79.
- Kinosternum subrubrum hippocrepis** 100 89.3  
(65-108 in 21) 89.6(67-111 in 20) YM 67.
- Lacerta agilis** 108 71.8(60-75) 77.6(60-82) IEF  
& SV 61.
- Lacerta agilis chersonensis** 99.5 70.4(60-82)  
70.1(61-84) IEF & SV 61.
- Lacerta melisellensis** 88 (63.4 in 16) (55.7 in  
40) EN, GG, MS, SYY, RC & VJ 72.
- Lacerta muralis** 101.8 58.7(51-63) 59.7(53-66)  
IEF & SV 61.
- Lacerta muralis maculiventralis** 99 59.3(57-62)  
58.8(57-61) IEF & SV 61.
- Lacerta pratincola** 116 47.1(41-51) 54.6(50.5-  
57) IEF & SV 61.
- Lacerta sicula** 90.0 62.6 in 31 56.0 in 42  
RM 64.
- Lacerta sicula alveaoi** 92 (68-70) (57-70) SB 70.
- Lacerta sicula ciclopica** 94 (70-75 in 10) (65-71  
in 7) RM 55.
- Lacerta sicula medemi** 88.3 (70-75) (60-68) in  
21 RM 55.
- Lacerta taurica** 82 55.5 45.5 IEF & SV 61.
- Lacerta tiliguerta eiselti** 91 57.4(53-60 in 6)  
52(49-55 in 4) BL 72.
- Lacerta tiliguerta maresi** 90 66.7(60-71 in 7)  
60.8(54-64 in 4) BL 72.
- Lacerta trilineata media** 103 110.7(101-131 in  
10) 113.6(100-137 in 10) JEF & RM 59.
- Lacerta trilineata trilineata** 105.4 107.7(104-  
131 in 10) 113.6(100-137 in 10) RM 59.
- Lacerta vauerselli** 102 52.4(46-60 in 21) 53.4  
(46-59 in 7) GFW 41.
- Lacerta viridis** 92.8 112.8(92-123 in 26) 104.4  
(93-119 in 24) RM & OS 49.
- Lacerta viridis chlornota** 91.9 115(100-127 in  
9) 105.3(98-116 in 6) SB 70.
- Lacerta vivipara** 116 45(42-48) 52(49-55) VFP  
& ASK 64.
- Lacerta wagleriana** 92.3 (52-76 in 40) (49-60  
in 68) SB 70.
- Lacerta wagleriana antoninoi** 87 (61-70 in 12)  
(52-60 in 13) SB 70.
- Lacerta wagleriana maritimensis** 87.8 (53-70 in  
23) (49-59 in 10) SB 70.
- Lampropeltis calligaster** 90.9 850.7(681-1185 in  
78) 773.2(568-1070 in 75) HSF°.
- Lampropeltis getulus** 87.1 1299.8(865-1607 in  
24) 1019(877-1485 in 9) FNB 21.
- Lampropeltis getulus boylii** 94.7 1077.3(919-  
1180 in 10) 1020.3(920-1220 in 12) FNB 21.
- Lampropeltis getulus holbrooki** 87.5 1067.2  
(790-1634 in 18) 933.6(765-1145 in 21)  
FNB 21.
- Lampropeltis multicincta** 112 507-850 547-  
973 AHW & AAW 57.
- Lampropeltis pyromelana** 91 424-1067 519-  
840 AHW & AAW 57.
- Lampropeltis triangulum** 87.8 821.5(710-1115  
in 17) 721.3(601-900 in 7) FNB 21.
- Lampropeltis triangulum elapsoides** 88.0 468.9  
(400-599 in 9) 412.5(355-482 in 13) FNB 21.
- Lampropeltis triangulum syspila** 96.6 578.3  
(420-797 in 47) 558.9(457-675 in 35) HSF°.
- Lapemis curtus** 100 828 827 ZH, TI & TO 74.
- Leimadophis reginae** 111.9 400.6(313-490 in  
32) 448.3(350-580 in 45) HSF°.
- Leimadophis taeniurus** 105.4 391.7(302-440 in  
7) 413.2(370-481 in 18) HSF°.
- Leiocephalus astictus** 85 69.2(58-79 in 15) 58.7  
(55-62 in 10) AS 59.

- Leiocephalus cubensis* 77 88.4(64-110 in 37) 68.0(56-81 in 28) AS 59.
- Leiocephalus exotheotus* 84 59.8(46-70 in 19) 49.9(43-57 in 16) AS 59.
- Leiocephalus gigas* 72 100.7(80-121 in 23) 72.1 (61-83 in 30) AS 59.
- Leiocephalus macropus felinoi* 70 73-87 in 8 54-59 in 8 AS 59.
- Leiocephalus pambasileus* 78 83.4(66-95 in 11) 65.4(64-67 in 7) AS 59.
- Leiocephalus paraphrus* 76 83.9(55-98 in 9) 63.7(56-69 in 17) AS 59.
- Leiocephalus raviceps klinkowskii* 89 58.5(53-69 in 4) 51.9(46-59 in 8) AS 60.
- Leiocephalus uzzelli* 82 66.5(61-71 in 23) 54.5(52-57 in 11) AS 60.
- Leiocephalus sierrae* 66 73.2(60-81 in 33) 62.8 (57-67 in 30) AS 59.
- Leiocephalus stictigaster* 83 66.1(57-79 in 26) 54.9(48-72 in 27) AS 59.
- Leioploisma rhomboidalis* 100 50.5(46-55 in 42) 50.5(48-56 in 33) DCW 63.
- Lepidodactylus lugubris* 102.1 36.9(35-39 in 6) 37.4(31-40 in 14) AHW 70.
- Leposoma guianensis* 103 35.6(30-37 in 8) 36.6 (30-39 in 14) MSH 73.
- Leposoma parietale* 105 33.0(29-38 in 53) 34.7 (31-39 in 24) WED ms.
- Leptodeira annulata* 107.5 509.5(442-580 in 52) 547.9(480-635 in 51) HSF°.
- Leptophis ahaetulla* 90.6 1021(848-1145 in 11) 928(815-1000 in 12) HSF°.
- Liolaemus anomalus* 91 (55-80 in 9) (54-72 in 7) JMC 79.
- Liolaemus archeforus* 90.5 74.4(69-87 in 10) 82.1(76-92 in 10) JMC 75.
- Liolaemus archeforus sarmentiori* 93.8 (80-85) (75-80) JMC 75.
- Liolaemus kingii* 91.6 77-100 in 14 72-90 in 14 JMC 75.
- Liophis miliaris* 123.8 539(382-738 in 123) 667(480-993 in 244) CG 64.
- Lipinia noctua* 101 43.7(37-49 in 22) 44.3 (41-49 in 22) TDS 80.
- Lycophidion capense* 133 343.2(310-391 in 6) 454.8(302-533 in 6) var.
- Mabuya bayoni* 105 68.8-72.6 in 8 70-80 in 15 RFL 64.
- Mabuya brachypoda* 100.6 72.5(64-84 in 8) 73.0(64-88 in 6) EHT 56.
- Mabuya buettneri* 120 71 85 RB 74.
- Mabuya mabouya* 112.1 71.6(66-91 in 21) 80.3 (72-91 in 18) HSF°.
- Mabuya mabouya alliacea* 105.8 70.8(66-76 in 10) 74.8(71-88 in 5) EHT 56.
- Mabuya maculilabris* 98 71.2(52-84 in 16) 69.9 (55-77 in 17) RFL 64.
- Mabuya multifasciata* 94 101.5(90-113) 95(87-103) RM 30.
- Mabuya occidentalis* 108 72 78 RBH & ERP 77.
- Mabuya punctata* 88 83.2(66-92 in 48) 72.1 (62-92 in 52) HT 46.
- Mabuya quinquetaeniata margaritifer* 88.1 262 (253-273 in 5) 230.9(220.5-241 in 6) VFMF 30 (total lengths).
- Mabuya sparsa* 86.5 73.5(61-85 in 13) 63.5 (66-85 in 21) CKB 69.
- Mabuya spilogaster* 104.4 67.0±.75 in 88 70.0±.62 in 131 RBH & ERP 77.
- Mabuya striata* 101.1 77.7(68.5-91 in 47) 78.6 (67.5-92 in 42) VFMF 30.
- Mabuya varia* 105.5 57.9(55-60 in 4) 61.0(53-70 in 5) var.
- Mabuya variegata* 111 35 39 RBH & ERP 77.
- Macrocchelys lacertina* 86.4 460(370-570 in 25) 397(33-50 in 33) JLD 71.
- Macropisthodon rufus* 139 558.0(543-590) 783.3(770-805) CHP 35.
- Malaclemys terrapin* 158 100-140 150-230 CHE & RWB 72.
- Malaclemys terrapin centrata* 143.5 115(100-123 in 13) 165(155-176 in 9) RS 80.
- Malaclemys terrapin tequesta* 140.5 123(109-144 in 26) 173(142-205 in 181) RS 80.
- Masticophis lateralis* 106 593 627 AHW & AAW 57.
- Masticophis taeniatus* 95.4 600-1050 575-1000 AHW & AAW 57.
- Masticophis taeniatus ruthveni* 95.6 1031 981 AHW & AAW 57.
- Maticora intestinalis* 98.6 487.4(426-560 in 5) 480.5(455-528 in 5) FK 41.
- Meroles cuneirostris* 90.6 54 49 SRG & MDR 79.
- Micrurus fulvius* 133.5 555(450-710 in 61) 740 (570-990 in 39) DRJ & RF 80.
- Micrurus fulvius tenere* 118.9 466(388-601 in 46) 554.2(355-950 in 92) HBQ 79.
- Moloch horridus* 113.2 84.6(79-96 in 31) 96.0 (82-110 in 33) ERP & HDP 70.
- Naja melanoleuca* 85 2040(1660-2692 in 4) 1732(1353-2591 in 4) var.
- Naja naja* 98.9 1048(928-1240 in 16) 1033 (943-1168 in 14) FK 41.
- Naja nigricollis* 102 1211(905-1555 in 9) 1148 (713-1470 in 7) var.
- Natriciteres olivacea* 125.4 328(287-382 in 5) 412(338-460 in 5) var.
- Natrix annularis* 137.5 411(340-500 in 49) 565 (475-695 in 27) TPM 50.
- Natrix natrix* 114 557.7(430-660) 634.4(420-830) IEF & SV 61.
- Natrix natrix sicula* 114.5 610(510-755 in 14) 699(525-1000 in 28) SB 70.
- Natrix percarinata* 136 564(530-638 in 6) 766 (620-1047 in 6) var.
- Natrix tessellata* 102.5 549(475-599) 562(472-641) IEF & SV 61.
- Natrix trianguligera* 117.8 607(405-956 in 23) 715(367-912 in 19) FK 41.
- Nerodia cyclopion* 124 626-900 660-1250 AHW & AAW 57.

- Nerodia erythrogaster bogerti* 107 618(539-708 in 4) 663(583-794 in 6) RC 69.
- Nerodia erythrogaster transversa* 115 686.2 (630-750 in 10) 786.8(664-966 in 10) RC 69.
- Nerodia fasciata* 116 600-1090 660-1300 AHW & AAW 57.
- Nerodia fasciata confluens* 132 410-658 500-910 AHW & AAW 57.
- Nerodia fasciata pictiventris* 152 425-818 700-1195 AHW & AAW 57.
- Nerodia rhombifera* 111 772.0(695-862 in 10) 859.7(774-1015 in 10) RC 69.
- Nerodia rhombifera blanchardi* 120 714.8(683-780 in 10) 854.6(692-1068 in 10) RC 69.
- Nerodia rhombifera werleri* 162 676.5(529-791 in 10) 1093(956-1162 in 10) RC 69.
- Nerodia sipedon* 132.4 551.2(413-748 in 55) 729.7(570-1025 in 46) HSF<sup>a</sup>.
- Nerodia sipedon insularum* 108 685-900 562-1151 AHW & AAW 57.
- Nerodia sipedon pleuralis* 124 670-1100 710-1350 AHW & AAW 57.
- Nerodia taxispilota* 117 670-1100 710-1350 AHW & AAW 57.
- Nerodia valida* 135 545.4(513-579 in 10) 738.5 (694-867 in 10) RC 69.
- Nerodia valida celaeno* 109 613.4(556-712 in 10) 671.1(608-730 in 10) RC 69.
- Nerodia valida isabelleae* 142 417.3(379-479 in 10) 591.4(531-707 in 10) RC 69.
- Nerodia valida thamnophisoides* 121 452.8(425-500 in 10) 547.2(476-672 in 10) RC 69.
- Neusticurus bicarinatus* 85 100(90-117 in 19) 85(79-96 in 15) MSH 73.
- Neusticurus equestris* 93.0 61(52.5-72 in 66) 56.6(53.5-60 in 23) WCS 75.
- Ninia maculata* 107.2 202.6(187-231 in 18) 217.4(187-233 in 7) HSF<sup>a</sup>.
- Notechis scutatus* 98.9 81.6 in 174 80.8 in 32 RS 77.
- Opheodrys aestivus* 100 345-379 335-805 AHW & AAW 57.
- Opheodrys major* 83.4 750.5(650-930 in 4) 626(610-678 in 4) var.
- Opheodrys vernalis* 101 332(304-358 in 6) 335(301-378 in 7) HMS 63.
- Ophiomorus persicus* 119 64.6(56-72 in 7) 77.1 (73-82 in 9) SCA & AEL 66.
- Ophiomorus Rathbuni* 112 77.7(64-85 in 7) 86 (63-99 in 11) SCA & AEL 66.
- Ophiomorus tridactylus* 103 82(71-91 in 9) 84.6(76-88 in 6) SCA & AEL 66.
- Ophisaurus attenuatus* 95.2 226.6(200-285 in 733) 215.6(195-263 in 420) HSF<sup>a</sup>.
- Oxybelis argenteus* 125 576(447-774 in 8) 724 (630-806 in 11) WED ms.
- Oxyrhopus melanogenys* 115.2 588(540-696 in 16) 677(605-755 in 18) HSF<sup>a</sup>.
- Oxyrhopus petola* 117.6 662.2(608-758 in 13) 779.3(700-857 in 14) HSF<sup>a</sup>.
- Pareas carinatus* 99.6 387.9(339-454 in 20) 386(332-460 in 20) FK 41.
- Pelamis platurus* 118 563(518-621 in 30) 664 (627-738 in 30) CK 75.
- Peropos mutilatus* 99 53.3(52.4-54.0 in 70) 52.8(52.5-53.0 in 98) CC 62.
- Philothamnus hoplogaster* 120.1 417.5(335-690 in 6) 501(398-655 in 4) var.
- Philothamnus irregularis* 133 601.6(499-730 in 8) 802.5(646-1070 in 6) var.
- Phrynocephalus scutellatus* 105.2 (42.5-48.0) (40.5-50.5) AEL 59.
- Phrynosoma cornutum* 106.6 69.6(64-75 in 15) 74.4(65-82 in 17) HSF<sup>a</sup>.
- Phrynosoma coronatum* 101.5 82.5(71-90 in 6) 83.6(74-96 in 5) HSF<sup>a</sup>.
- Phrynosoma douglassi* 109.7 60.9(39-88 in 11) 66.9(28-94 in 23) WWT & BHB 66.
- Phrynosoma modestum* 112.2 55.8(51-66 in 6) 62.8(55-71 in 10) HSF<sup>a</sup>.
- Phrynosoma orbiculare* 103 73.5(64-86 in 8) 75.7(68-90 in 15) HSF<sup>a</sup>.
- Phrynosoma platyrhinos* 106.2 71.5(65-75 in 24) 76(65-80 in 32) ERP & WSP 75.
- Phrynosoma solare* 108 90.4(80-100 in 19) 98 (80-110 in 22) WSP 71.
- Phyllodactylus angustidigitatis* 95.1 50.3(41-57) 47.8(37-54) in 246 JRD & RBH 70.
- Phyllodactylus europaeus* 97.5 40.8(40-44 in 4) 39.8(38-42 in 5) SB 68.
- Phyllodactylus gerrhopygus* 97.5 43.9(32-56) 42.8(32-55) in 98 JRD & RBH 70.
- Phyllodactylus inaequalis* 99.5 37.0(33-40) 36.8 (30-42) in 59 JRD & RBH 70.
- Phyllodactylus interandinus* 104.9 39.2(32-45) 41.1(33-47) in 149 JRD & RBH 70.
- Phyllodactylus johnwrighti* 103 37.9(32-40) 39.0(33-44) in 41 JRD & RBH 70.
- Phyllodactylus kofordi* 101.7 38.0(30-45) 38.6 (30-46) in 167 JRD & RBH 70.
- Phyllodactylus lepidopygus* 114.7 40.8(32-50) 46.8(36-55) in 63 JRD & RBH 70.
- Phyllodactylus microphyllus* 99.8 46.7(33-56) 46.5(32-58) in 277 JRD & RBH 70.
- Phyllodactylus reissi* 97.0 59.4(42-75) 57.5(37-73) in 772 JRD & RBH 70.
- Phyllodactylus tuberculosus* 102 72.5(54-80) 76.6(72-83) GAH & JRL 67.
- Phyllodactylus ventralis* 99.8 62.4(50-74) 62.3 (52-75) in 22 JRD & RBH 70.
- Phyllorhynchus decurtatus nubilus* 110 300-343 in 50 300-408 in 33 AHW & AAW 57.
- Phyllorhynchus decurtatus perkinsi* 97 340 in 214 330 in 148 AHW & AAW 57.
- Pituophis melanoleucus affinis* 104 676 in 31 698 in 23 AHW & AAW 57.
- Pituophis melanoleucus catenifer* 95 1060(760-1360) 1010(750-1270) AHW & AAW 57.
- Pituophis melanoleucus deserticola* 91 910.5 in 23 826.2 in 13 AHW & AAW 57.
- Pituophis melanoleucus sayi* 101.0 1246(1015-1779 in 59) 1258(1005-1624 in 55) HSF<sup>a</sup>.
- Plica plica* 100 90-140 83-143 RE 70.

- Plica umbra* 90.5 (72-100 in 15) (61-94 in 14)  
RE 70.
- Plica umbra ochrocollaris* 102.8 78.5(66-89 in 16) 80.6(69-90 in 12) WED ms.
- Polychrus marmoratus* 124 385 in 9 478 in 13  
WB 44.
- Prionodactylus argulus* 99.5 38.0(30-42 in 14)  
37.8(32-47 in 25) WED ms.
- Prionodactylus manicatus* 122.8 51.3(41-65 in 6) 63(55-70 in 5) WED ms.
- Proctoporus boliviensis* 106 50.0(46-61 in 10)  
53.0(46-61 in 10) HSF\*.
- Prosymna ambigua* 117 234(202-250 in 4) 274  
(216-366 in 4) var.
- Psammodynastes pulverulentus* 109 374(335-426 in 9) 407(352-485 in 12) FK 41.
- Psammophis schokari* 77.4 664(614-737 in 10)  
513(443-600 in 5) HM 58.
- Psammophis sibilans* 81.9 886(708-1215 in 19)  
725(516-1253 in 18) var.
- Psammophylax tritaeniatus* 93 622.7(525-734 in 8) 579(467-851 in 10) var.
- Pseudechis porphyriaca* 95.4 1116 in 225 1061  
in 55 RS 77.
- Pseudemys concinna* 117 145 170 RBB 79.
- Pseudemys floridana* 138.5 164(110-200 in 11)  
227.5(200-260 in 16) JWG & JWC 77.
- Pseudemys floridana "suwanensis"* 143 150-270  
in 208 240-360 in 232 AC 52.
- Pseudemys rubriventris* 116 257(212-277 in 4)  
299(281-322.5 in 9) AEC 52; TEG 71.
- Pseudemys scripta* 140 217(137-340 in 98) 304  
(248-349 in 48) EOM & JML 71.
- Pseudemys scripta troostii* 108 140-210 in 9  
172-206 in 6 AC 52.
- Pseudocerastes fieldi* 108 575 in 8 623 in 7  
HM 65.
- Pseudogonatodes guianensis* 102 25.2(23-26 in 8) 25.5(23-27 in 8) WED ms.
- Ptenopus garrulus* 101.1 45.6(33.0-48.0 in 5)  
46.1(32.5-49.5 in 4) var.
- Ptyas korros* 92.2 1021(771-1227 in 15) 940  
(793-1055 in 19) FK 41.
- Ptyas mucosus* 93.8 1300(1120-1490 in 10)  
1220(1050-1507 in 14) FK 41.
- Ptychoglossus brevifrontalis* 111 (40-46) (42-53) in 10 JRD & PS 75.
- Regina allenii* 106 401-600 401-652 AHW &  
AAW 57.
- Regina grahami* 119.5 478(340-620 in 36) 571  
(430-760 in 33) RJH 69.
- Regina rigida* 134 350-546 493-705 AHW &  
AAW 57.
- Regina septemvittata* 114.1 395 in 68 451 in  
58 JTW & WED 50.
- Rhabdophis chrysargyra* 106 473(417-590 in 94)  
500(420-643 in 110) CPJH 41.
- Rhabdophis subminiata* 122 388(352-445 in 43)  
467(430-529 in 47) CPJH 41.
- Rhabdophis tigrinus* 120 600-900 700-1100 HF  
65.
- Rhadinea flavilata* 111.5 205 in 46 229 in 45  
CWM 74.
- Rhamphiophis acutus* 86.5 651.2(549-826 in 4)  
564(400-729 in 4) var.
- Rhinocheilus lecontei* 87 498-936 536-820  
AHW & AAW 57.
- Rhinocheilus lecontei clarus* 91 642 in 29 586  
in 13 AHW & AAW 57.
- Rhinoclemmys pulcherrima incisa* 117 153 in 5  
179 in 5 HH ms.
- Salvadora hexalepis* 90 684-1014 709-826  
AHW & AAW 57.
- Salvadora hexalepis mojavensis* 84 800-941  
650-803 AHW & AAW 57.
- Salvadora hexalepis virgultea* 91 678-1027 625-  
892 AHW & AAW 57.
- Salvadora lemniscata* 97.4 1460 in 10 1423 in  
10 CMB 39.
- Salvadora mexicana* 87 1246 in 10 1083 in 10  
CMB 39.
- Sauromalus obesus* 92 175(162-197 in 25) 161  
(149-184 in 28) SRJ 65.
- Sceloporus adleri* 92 65.3(59-72 in 14) 60.4  
(54-66 in 14) HSF 78.
- Sceloporus bulleri* 97 100.7(95-116 in 10) 97.7  
(91-108 in 10) HSF 78.
- Sceloporus chrysostictus* 95 54.0(45-62 in 81)  
51.3(44-61 in 82) HSF 78.
- Sceloporus clarkii* 92 102.1(97-118 in 29) 94.9  
(88-107 in 21) HSF 78.
- Sceloporus clarkii boulengeri* 81 104(91-138 in  
27) 84.1(72-120 in 36) HSF 78.
- Sceloporus cozumelae* 87 50.7(43-60 in 57)  
45.5(41-57 in 33) HSF 78.
- Sceloporus cyanogenys* 105 100.7(86-116 in 8)  
105.9(88-119 in 22) HSF 78.
- Sceloporus formosus* 103 71.6(64-80 in 12)  
73.9(68-80 in 8) HSF 78.
- Sceloporus graciosus* 104 57.4(52-63 in 106)  
59.9(53-69 in 121) HSF 78.
- Sceloporus graciosus "gracilis"* 103 52.1(49-61  
in 85) 53.9(48-63 in 76) HSF 78.
- Sceloporus graciosus vandenburgianus* 95 60.2  
(55-65 in 34) 57.5(51-63 in 26) HSF 78.
- Sceloporus grammicus* 96 51.2(42-57 in 23)  
49.3(44-54 in 32) HSF 78.
- Sceloporus insignis* 92 89.5(80-99 in 10) 82.6  
(80-89 in 10) HSF 78.
- Sceloporus jarrovi* 91 78.8(61-91 in 35) 71.88  
(57-86 in 33) HSF 78.
- Sceloporus lundelli* 105 90.0(86-93 in 4) 94.7  
(91-99 in 6) HSF 78.
- Sceloporus magister* 84 115.5(80-140 in 42)  
96.6(80-120 in 33) HSF 78.
- Sceloporus malachiticus* 95 79.1(67-90 in 146)  
75.5(64-86 in 208) HSF 78.
- Sceloporus megalepidurus* 99 45.2(42-50 in 10)  
44.9(41-48 in 11) HSF 78.
- Sceloporus merriami* 95 52.3(45-61 in 60) 49.8  
(44-55 in 51) HSF 78.
- Sceloporus merriami annulatus* 95 47.7(42-53  
in 96) 45.3(39-50 in 62) HSF 78.

- Sceloporus mucronatus* 95 93.3(85-100 in 21)  
88.5(81-100 in 17) HSF 78.
- Sceloporus nelsoni* 87 60.1(53-65 in 26) 52.1  
(48-58 in 21) HSF 78.
- Sceloporus occidentalis* 106 66.1(61-72 in 23)  
70.4(68-77 in 13) HSF 78.
- Sceloporus occidentalis biseriatus* 107 73.6(65-  
81 in 14) 82.7(72-87 in 21) HSF 78.
- Sceloporus olivaceus* 111 82.9(60-93 in 34)  
93.0(63-107 in 107) HSF 78.
- Sceloporus orcutti* 90 102(90-115 in 17) 92  
(85-106 in 77) HSF 78.
- Sceloporus pictus* 98 48.9(47-51 in 8) 47.9  
(44-52 in 7) HSF 78.
- Sceloporus poinsetti* 86 116.4(100-130 in 18)  
97.0(86-116 in 21) HSF 78.
- Sceloporus pyrocephalus* 85 62.9(58-68 in 9)  
53.5(49-60 in 12) HSF 78.
- Sceloporus scalaris* 111 45.3(40-55 in 45) 51.3  
(40-60 in 203) HSF 78.
- Sceloporus scalaris aeneus* 99 46.1(42-49 in 10)  
45.5(41-53 in 23) HSF 78.
- Sceloporus scalaris bicanthalis* 106 45.4(43-50  
in 14) 48.8(42-55 in 11) HSF 78.
- Sceloporus siniferus* 86 60.8(53-67 in 32) 52.3  
(48-61 in 35) HSF 78.
- Sceloporus smaragdinus* 93 67.2(60-80 in 14)  
62.2(55-77 in 17) HSF 78.
- Sceloporus spinosus* 99 88.3(82-99 in 17) 87.2  
(77-96 in 18) HSF 78.
- Sceloporus taeniocnemis* 97 71.1(65-81 in 19)  
68.7(60-82 in 20) HSF 78.
- Sceloporus teapensis* 93 58.9(46-64 in 24) 52.0  
(47-62 in 26) HSF 78.
- Sceloporus torquatus* 99 103.5(98-118 in 13)  
102.7(97-110 in 9) HSF 78.
- Sceloporus undulatus* 110 56.1(47-65 in 59)  
62.1(53-70 in 35) HSF 78.
- Sceloporus undulatus consobrinus* 101 60.3(55-  
74 in 45) 61.0(55-71 in 46) HSF 78.
- Sceloporus undulatus elongatus* 112 63.1(55-  
71 in 20) 72.0(65-83 in 20) HSF 78.
- Sceloporus undulatus erythrocheilus* 110 59.5  
(53-65 in 21) 66.2(60-72 in 21) HSF 78.
- Sceloporus undulatus garmani* 107 52.2(45-59  
in 62) 56.3(53-68 in 44) HSF 78.
- Sceloporus undulatus hyacinthinus* 107 59.8  
(57-63 in 18) 64.2(57-67 in 11) HSF 78.
- Sceloporus undulatus tristichus* 107 58.6(52-  
70 in 33) 62.8(57-75 in 53) HSF 78.
- Sceloporus utiformis* 93 64.4(58-75 in 9) 59.7  
(51-66 in 10) HSF 78.
- Sceloporus variabilis* 81 65.8(57-74 in 97) 53.1  
(44-68 in 157) HSF 78.
- Sceloporus virgatus* 112 52.0(48-58 in 11) 58.8  
(51-69 in 11) HSF 78.
- Sceloporus woodi* 106 47.6 50.5 HSF 78.
- Scincella lateralis* 105.3 45.4(43-50 in 14) 47.8  
(42-56 in 22) HSF<sup>o</sup>.
- Scincus mitratus* 79.1 126(121-134 in 4) 99.7  
(92-105 in 5) ENA & AEL 77.
- Scincus scincus* 85.2 116(88-139 in 27) 99(83-  
115 in 29) ENA & AEL 77.
- Seminatrix pygaea* 110 303.3(275-336 in 20)  
330.3(285-415 in 20) HGD 50.
- Sistrurus catenatus* 92 663 in 10 610 in 10  
LMK 37.
- Sistrurus rarus exiguus* 76 587-664 in 13 413-  
481 in 4 JAC & BLA 79.
- Sonora episcopa* 99.7 213.5(181-258 in 20)  
213.1(180-245 in 16) HSF<sup>o</sup>.
- Sonora michoacanensis* 104.1 234.4(205-275 in  
5) 244(234-272 in 6) ACE 73.
- Sonora semiannulata* 99 211 in 43 209 in 57  
AHW & AAW 57.
- Spalerosophis cliffordi* 107 1009(725-1265 in  
164) 1165(780-1520 in 205) RD 67.
- Sphaerodactylus argivus* 99.3 25.4(22-29 in 82)  
25.2(21-29 in 106) RT 75.
- Sphaerodactylus argus* 113 29.1(26-33 in 65)  
32.5(28-33 in 71) RT 75.
- Sphaerodactylus argus barstchi* 105.8 25.8(20-  
29 in 30) 27.3(24-29 in 17) RT 75.
- Sphaerodactylus lewisi* 107.5 24.5(22-27 in 12)  
26.4(24-27 in 15) RT 75.
- Sphaerodactylus oxyrhinus* 111.2 30.9(28-33 in  
12) 34.4(29-34 in 14) RT 75.
- Sphaerodactylus oxyrhinus dacnicolor* 101.5  
29.8(27-32 in 28) 30.3(27-32 in 30) RT 75.
- Sphaerodactylus semasiops* 110 25.4(23-30 in  
10) 28.0(24-31 in 16) RT 75.
- Sphenomorphus cherriei* 99.8 54.7(50-58 in 39)  
54.6(49-63 in 61) HSF<sup>o</sup>.
- Sternotherus carinatus* 98 105(84-116 in 18)  
103(82-117 in 13) YM 67.
- Sternotherus minor* 105 82.3 in 310 86.3 in 341  
JBI 77.
- Sternotherus odoratus* 105 73.7(64-85 in 18)  
77.5(66-84 in 16) YM 67.
- Stilosoma extenuatum* 104 270-567 300-575  
AHW & AAW 57.
- Storeria dekayi taxexanum* 120.2 203.8(167-244 in  
13) 245.0(201-309 in 18) HSF<sup>o</sup>.
- Storeria dekayi vieta* 119.8 191(175-290 in 34)  
227(175-412 in 22) HT 44.
- Storeria occipitomaculata* 118.4 168.5(141-203  
in 14) 199.5(177-272 in 15) HSF<sup>o</sup>.
- Tachymenis chilensis assimilis* 87 306 267  
WFW 45.
- Tachymenis chilensis melanura* 106 350 372  
WFW 45.
- Tachymenis peruviana* 93 333 309 WFW 45.
- Tantilla gracilis* 125.7 141.4(121-165 in 43)  
177.9(120-209 in 21) HSF<sup>o</sup>.
- Tantilla planiceps* 94 277-375 211-373 AHW  
& AAW 57.
- Tarentola mauritanica* 84 62.7±2.3 52.7±1.1  
JR & PB 71.
- Telescopus semiannulatus* 128.2 615.5(478-760  
in 4) 790.2(522-953 in 4) var.
- Terrapene carolina* 90.9 140.1(128-154 in 8)  
127.4(109-142 in 9) WED & AS 58.
- Terrapene coahuila* 92.5 108.9 in 70 100.9 in  
94 WSB 71.

- Terrapene ornata* 101.8 111.6(100-126 in 75) 113.5(101-130 in 163) HSF°.
- Testudo graeca* 97 208.7(145-270) 203.2 IEF & SV 61.
- Thamnophis brachystoma* 112 290-440 290-506 AHW & AAW 57.
- Thamnophis butleri* 109 338(310-410 in 92) 369(310-480 in 60) CCC 52.
- Thamnophis couchi* 132 430-580 440-900 AHW & AAW 57.
- Thamnophis couchi gigas* 134 500-740 550-1080 AHW & AAW 57.
- Thamnophis couchi hammondi* 136 373-729 388-989 AHW & AAW 57.
- Thamnophis couchi hydrophilus* 130 330-580 350-610 AHW & AAW 57.
- Thamnophis cyrtopsis* 146 429-470 504-764 AHW & AAW 57.
- Thamnophis elegans* 118 370-590 420-690 AHW & AAW 57.
- Thamnophis elegans biscutatus* 138 490-797 570-922 AHW & AAW 57.
- Thamnophis elegans terrestris* 106 308-604 380-590 AHW & AAW 57.
- Thamnophis elegans vagrans* 122 453(290-580 in 35) 586(470-730 in 36) HSF 40.
- Thamnophis eques* 115 412(321-489 in 6) 498 (407-518 in 6) var.
- Thamnophis marcianus* 126 335-621 322-887 AHW & AAW 57.
- Thamnophis ordinoides* 125 328(250-500 in 151) 410(280-550 in 125) HSF 40.
- Thamnophis proximus* 109.5 489.6(420-600 in 13) 536.5(445-760 in 31) HSF°.
- Thamnophis radix* 108 325-650 350-700 AHW & AAW 57.
- Thamnophis sauritus* 117.5 410(360-540 in 115) 483(360-610 in 158) CCC 52.
- Thamnophis sirtalis* 114 453(390-600 in 240) 515(390-720 in 235) CCC 52.
- Thamnophis sirtalis parietalis* 123 519(412-683 in 215) 636(510-968 in 282) HSF°.
- Thamnophis sirtalis pickeringi* 124 471.4±10.84 584.40±13.10 WBI 36.
- Thecadactylus rapicaudus* 106 101(93-108 in 5) 107(97-116 in 6) WED ms.
- Thelotornis capensis* 100 945(757-1312 in 5) 942(670-1366 in 5) var.
- Thrasops jacksoni* 125.5 1322(1300-1330 in 5) 1661(1263-1550 in 6) var.
- Tretanorhinus nigroluteus* 141 423 in 23 597 in 18 RWH & LCH 79.
- Tretioscincus agilis* 107 37.9(33-48 in 70) 40.7 (35-48 in 53) PEV & RR 69.
- Trimeresurus albolabris* 161 468(438-485 in 5) 751(710-786 in 5) CHP 35.
- Trimeresurus flavoviridis* 89.3 1035(720-1370 in 24) 925(530-1370 in 22) KM 79.
- Trimeresurus okinavensis* 99 517(300-676 in 20) 511(310-700 in 21) KM 79.
- Trimeresurus puniceus* 138.7 429(360-499 in 4) 595(527-656 in 4) FK 41.
- Trimeresurus stejnegeri* 109.1 631.5(592-670 in 4) 690.8(625-731 in 4) CHP 35.
- Trimorphodon biscutatus lambda* 130 296-788 359-1026 AHW & AAW 57.
- Trimorphodon biscutatus vandenburgi* 127 555-738 556-1054 AHW & AAW 57.
- Trionyx muticus* 157.5 98.1(80-120 in 1105) 154.5(140-180 in 164) MVP 77.
- Trionyx spiniferus emoryi* 236 80-90 200 RBB 79.
- Trionyx spiniferus ferox* 168 155(114-190 in 73) 286(165-395 in 98) WJB 55.
- Trionyx spiniferus pallidus* 182 90-100 160-185 RBB 79.
- Trogonophis wiegmanni* 98 179(165-196 in 6) 175(170-185 in 6) JB & HStG 63.
- Tropidoclonion lineatum* 122.2 215.1(183-247 in 19) 262.8(216-341 in 40) HSF°.
- Tropidurus albemarlensis* 79 82(65-95 in 67) 65(45-75 in 118) CCC 70.
- Tropidurus albemarlensis barringtonensis* 84 94(75-125 in 49) 79(55-85 in 31) CCC 70.
- Tropidurus bivittatus* 78 81(65-105 in 27) 63 (45-95 in 26) CCC 70.
- Tropidurus delanonis* 76 119(115-155 in 41) 90(85-115 in 43) CCC 70.
- Tropidurus duncanensis* 89 87(55-105 in 17) 77(55-85 in 32) CCC 70.
- Tropidurus grayi* 116 70.3(55-95 in 42) 81.4 (45-85 in 17) CCC 70.
- Tropidurus habeli* 79 107.1(95-115 in 23) 84.6 (75-95 in 27) CCC 70.
- Tropidurus icae* 86.7 85.6(77-94) 74.2(70-76) JRD & JWW 75.
- Tropidurus occipitalis* 81 64.4(50-75) 52.2(47-58) JRD & JWW 75.
- Tropidurus pacificus* 87 87.5(65-105 in 17) 75.7 (65-85 in 32) CCC 70.
- Tropidurus peruvianus* 86 98.3(90-103) 84.6 (78-97) JRD & JWW 75.
- Tropidurus salinicola* 92 62.3(51-72) 57.1(50-64) JRD & JWW 75.
- Tropidurus stolzmanni* 71.3 80.3(52-106) 57.4 (48-68) JRD & JWW 75.
- Tropidurus talarae* 77.8 81.6(77-84) 63.4(60-70) JRD & JWW 75.
- Tropidurus thoracicus* 87 68.5(63-74) 62(48-76) JRD & JWW 75.
- Tropidurus torquatus* 80 109.8(97.8-121.7 in 11) 88.1(79.5-98.5 in 7) RV & BSD 60.
- Typhlosaurus garipensis* 105.5 116.1±.78 in 37 122.9±.77 in 35 RBH & ERP 74.
- Typhlosaurus lineatus* 105 130.5±.64 in 133 137.3±.75 in 93 RBH & ERP 74.
- Typhlops angolensis adolfi* 124.5 377(281-534 in 11) 469.4(380-602 in 10) RFL 56.
- Typhlops angolensis dubius* 136.2 433(316-547 in 10) 591.7(464-703 in 6) RFL 56.
- Typhlops angolensis iraci* 141 396.5(312-532 in 4) 559(500-630 in 10) RFL 56.
- Uma inornata* 79.4 102(80-122 in 191) 81(70-99 in 213) WWM 65.

- Uma notata** 79 96(80-121 in 270) 76(70-94 in 214) WWM 66B.
- Uma scoparia** 85.6 97(80-113 in 248) 83(70-112 in 236) WWM 66A.
- Uracentron flaviceps** 70.4 49.8(42-58 in 4) 35.0 (30-42 in 5) CMF & TDS 68.
- Urechis gouldi** 83.4 36.2 in 129 30.2 in 29 RS 77.
- Urosaurus ornata** 97.3 49.6(41-64 in 178) 48.3 (40-62 in 129) HSF<sup>a</sup>.
- Uta antigua** 92 50.8±1.3 in 33 46.6±.90 in 27 AED, DWT & JWG 78.
- Uta mearnsi** 96 77.0(66-84 in 38) 73.9(132-172 in 50) MLH 65.
- Uta nolascensis** 93 50.05±1.07 in 21 46.6±.83 in 15 AED, DWT & JWG 78.
- Uta palmeri** 91 66.97±2.82 in 34 60.7±1.36 in 51 AED, DWT & JWG 78.
- Uta squamata** 93 50.6±1.03 in 25 47.1±.66 in 27 AED, DWT & JWG 78.
- Uta stansburiana** 87 (43-57 in 447) (40-56 in 402) HSF<sup>a</sup>.
- Varanus acanthurus** 86.6 170(153-192 in 6) 147.5(133-163 in 4) RM 58.
- Vermicella annulata** 139 392(282-534 in 84) 544(325-746 in 80) RS 80A.
- Vipera ammodytes** 118 (52-80) (61-95) SB 67B.
- Vipera berus** 108 462.5 in 100 498 in 127 IP 71.
- Vipera latastei** 90.1 333(270-400 in 12) 290 (250-340 in 6) HSG 73.
- Vipera ursini** 110 390 430 SB 67.
- Vipera xanthina** 95 937(810-1073 in 21) 894 (831-1100 in 33) HM 65.
- Virginia striatula** 115.7 180.8(182-200 in 90) 209.1(182-236 in 55) DRC 64.
- Virginia valeriae** 124.4 169.8(133-189 in 10) 211.3(190-240 in 15) HSF<sup>a</sup>.
- Xantusia henshawi** 110.7 56 62 JCL 75.
- Xenochrophis cerasogaster** 152.8 441.8(390-498 in 4) 673.2(480-754 in 4) EVM & SAM 65; MAS 43.
- Xenochrophis piseator** 134.8 423.8(300-570 in 20) 571.4(326-842 in 40) FK 41.
- Xenochrophis vittata** 123.9 327(263-386 in 12) 405(303-483 in 14) FK 41.
- Xenodermus javanicus** 111 345(316-418 in 15) 383(314-440 in 24) FK 41.
- Xenodon severus** 96.1 905(710-1325 in 19) 870(710-1129 in 15) HSF<sup>a</sup>.



## APPENDIX II

Maximum sizes (snout-vent) of reptiles recorded  
by various authors

Symbol(s) after each name represent(s) degree of size difference between the sexes (see p. 4); these are followed by male length and female length in millimeters, initials of authority, and year of publication.

- Ablepharus smithi* X 41, 42, GFW 53  
*Acrochordus javanicus* +++++ 900, 1515, MAS 43  
*Agama atra* —— 135, 108, VFMF 43  
*Agama cyanogaster* —— 167, 127, AEL 53  
*Agama hispida aculeata* — 110, 103, VFMF 43  
*Agama kirki* — 105, 92, AEL 53  
*Agama mossambica* —— 93, 70, VFMF 43  
*Agama planiceps* — 112, 102, VFMF 43  
*Akistrodon acutus* + 1130, 1250, CHP 35  
*Akistrodon blomhoffi brevicaudus* X 620, 598, HKG 77  
*Akistrodon blomhoffi siniticus* X 588, 608, HKG 77  
*Akistrodon caliginosus* X 521, 520, HKG 77  
*Akistrodon halys cognatus* — 590, 518, HKG 77  
*Akistrodon himalayanus* X 505, 520, MAS 43  
*Akistrodon rhodostoma* +++ 545, 765, MAS 43  
*Akistrodon saxatilis* — 689, 613, MAS 43  
*Ahaetulla nasuta* +++++ 795, 1220, MAS 43  
*Ahaetulla pulverulenta* +++++ 655, 1020, MAS 43  
*Amblyodipsas polylepis* +++++ 495, 1040, DGB & EVC 75  
*Amblyodipsas ventrimaculatus* ++ 290, 340, DGB & EVC 75  
*Ameiva chaitzami* — 85, 75, ACE 71  
*Ameiva undulata amphigrama* X 101, 104, HMS & LEL 46  
*Ameiva undulata gaigeae* —— 125, 107, HMS & LEL 46  
*Ameiva undulata hartwegi* —— 138, 115, HMS & LEL 46  
*Ameiva undulata parva* — 109, 95, HMS & LEL 46  
*Ameiva undulata podarga* —— 116, 96, HMS & LEL 46  
*Amphiesma beddomei* ++ 385, 480, MAS 43  
*Amphiesma craspedogaster* + 435, 490, MAS 43  
*Amphiesma khasiensis* + 375, 410, MAS 43  
*Amphiesma modesta* +++ 365, 460, MAS 43  
*Amphiesma monticola* ++ 262, 325, MAS 43  
*Amphiesma platyceps* — 655, 570, EVM 66  
*Amphiesma popei* X 438, 446, EVM 66  
*Amphiesma pryeri* ++ 607, 710, EVM 66  
*Amphiesma sieboldi* +++ 729, 943, EVM 66  
*Amphiesma venningi* + 410, 455, MAS 43  
*Amphiesma vibakari* X 551, 580, MAS 43  
*Amphiesma xenura* X 440, 430, MAS 43  
*Anguis fragilis* + 212, 232, var.  
*Anilius scytale* +++++ 810, 1184, JRD & PS 77  
*Anolis ahli* —— 58, 45, RR & EEW 61  
*Anolis alumina* — 40, 37, PEH 76  
*Anolis bahorucoensis southerlandi* —— 51, 44, AS 78  
*Anolis baleatus* —— 180, 148, AS 74  
*Anolis baleatus litorisilva* —— 158, 131, AS 74  
*Anolis baleatus multistruppus* — 150, 141, AS 74  
*Anolis baleatus scelestus* —— 180, 147, AS 74  
*Anolis barkeri* —— 98, 79, JPK 65  
*Anolis baronhae* — 158, 148, AS 74  
*Anolis dolichocephalus sarmenticola* —— 51, 42, AS 78  
*Anolis dolichocephalus portusalus* —— 52, 43, AS 78  
*Anolis extremus* —— 74, 60, EEW 72  
*Anolis hendersoni ravidormitans* — 49, 42, AS 78  
*Anolis homolechis cuneus* —— 58, 41, AS 68  
*Anolis homolechis jubar* —— 54, 40, AS 68  
*Anolis homolechis oriens* —— 56, 42, AS 68  
*Anolis homolechis quadriocellifer* —— 55, 40, AS 68  
*Anolis lividus* —— 69, 55, EEW 72  
*Anolis luciae* —— 91, 62, EEW 72  
*Anolis mestrei* —— 55, 44, RR & EEW 61  
*Anolis monticola* —— 56, 42, EEW 74  
*Anolis nubilus* —— 79, 52, EEW 72  
*Anolis oculatus* —— 75, 55, EEW 72  
*Anolis oculatus cabritensis* —— 75, 57, EEW 72  
*Anolis oculatus montanus* —— 95, 64, EEW 72  
*Anolis oculatus winstoni* —— 77, 61, EEW 72  
*Anolis petersi* + 102, 108, HSF 76  
*Anolis ricordi subsolans* X 152, 150, AS 74  
*Anolis ricordi viculus* — 148, 141, AS 74  
*Anolis rubribarbis* —— 58, 42, RR & EEW 61  
*Anolis rupinæ* —— 56, 42, EEW & IPW 74  
*Anolis sabanus* —— 67, 51, EEW 72  
*Aparallactus capensis* + 235, 268 DGB & EVC 75  
*Aparallactus guentheri* + 345, 380, DGB & EVC 75  
*Aparallactus jacksoni* X 228, 213, CRSP 74  
*Aparallactus ubangensis* ++ 375, 412, GW & AL 47  
*Aparallactus ulugurensis* X 320, 335, GW & RL 47  
*Argyrogena fasciolata* X 765, 790, MAS 43

- Arizona elegans* X 1168, 1165, LMK 46  
*Aristelliger georgeensis* —— 108, 83, AS & RIC 75  
*Aristelliger hechti* —— 90, 75, AS & RIC 75  
*Aristelliger lar* —— 132, 111, AS & RIC 75  
*Aristelliger praesignis* —— 85, 65, AS & RIC 75  
*Arrhyton dolichurum* — 308, 265, AS 65  
*Arrhyton taeniatum* + 401, 448, AS 65  
*Arrhyton vittatum* — 193, 179, AS 65  
*Arrhyton vittatum landoi* + 236, 250, AS 65  
*Aspidelaps scutatus* + 590, 640, DGB & EVC 75  
*Aspidura copei* + 340, 365, MAS 43  
*Aspidura trachyprocta* +++++ 350, 505, MAS 43  
*Atractia stokesii* +++ 1030, 1410, MAS 43  
*Atractaspis congica* — 441, 400, RL 50  
*Atractaspis dahomeyensis* + 417, 458, RL 50  
*Atractaspis microlepidotus* — 690, 525, RL 50  
*Atractaspis microlepidotus fallax* X 680, 705, RL 50  
*Atractaspis microlepidotus micropholis* —— 690, 525, RL 50  
*Atractus* "species A" + 395, 425, JRD & PS 77  
*Atractus badius* ++ 342, 413, JRD & PS 77  
*Atractus latifrons* +++ 446, 586, JRD & PS 77  
*Atractus resplendens* + 333, 372, JMS 60  
*Atractus roulei* ++ 330, 396, JMS 60  
*Atheris nitschei* ++ 523, 616, CRSP 74  
  
*Balanophis ceylonensis* — 390, 365, MAS 43  
*Bitis atropos* + 397, 434, VFMF 62  
*Bitis caudalis* X 417, 399, VFMF 62  
*Bitis cornuta* —— 347, 271, VFMF 62  
*Bitis gabonica* ++ 990, 1219, KPS 23  
*Bitis nasicornis* +++ 812, 966, KPS 23  
*Bitis paucisquamata* + 218, 234, VFMF 62  
*Bitis peringueyi* ++ 245, 297, RM 55  
*Blythia reticulata* +++ 275, 365, MAS 43  
*Boaedon fuliginosa* +++ 519, 810, CRSP 74  
*Boaedon olivaceus* X 596, 596, CRSP 74  
*Boiga blandingii* + 1635, 1833, CRSP 74  
*Boiga ceylonensis* +++ 780, 1095, MAS 43  
*Boiga cyanea* +++ 1060, 1420, MAS 43  
*Boiga cynodon* ++ 1110, 1310, MAS 43  
*Boiga forsteni* — 1460, 1260, MAS 43  
*Boiga gokool* + 630, 695, MAS 43  
*Boiga multimaculata* +++ 610, 800, MAS 43  
*Boiga ochracea* + 815, 885, MAS 43  
*Boiga trigonata* ++ 685, 810, MAS 43  
*Bothrops bilineatus* +++ 490, 638, JRD & PS 77  
*Bothrops neuwiedii* X 779, 800, RV & BSS 60  
*Bungarus bungaroides* —— 1240, 870, MAS 43  
*Bungarus candidus* — 1225, 1080, FK 41  
*Bungarus fasciatus* — 1005, 901, FK 41  
*Bungarus multicinctus* — 960, 825, CHP 35  
*Bungarus walli* — 1450, 1310, MAS 43  
  
*Calamaria leucogaster* + 196, 207, RFI & HM 65  
*Calamaria linnaei* ++ 308, 379, RFI & HM 65  
*Calamaria modesta* ++ 366, 428, RFI & HM 65  
*Calamaria septentrionalis* ++ 319, 371, RFI & HM 65  
*Calamaria uniformis* + 281, 320, MAS 43  
*Calliophis calligaster* — 519, 476, AEL 63  
*Calliophis calligaster gemianulus* — 519, 451, AEL 63  
*Calliophis japonicus* —— 533, 435, KK, DK, TF & KT 77  
*Calliophis maclellandi* +++ 565, 720, MAS 43  
*Calliophis maculiceps* ++ 385, 447, MAS 43  
*Calopistes maculatus* — 173, 148, RDB 66  
*Calotes versicolor* — 95, 82.5, MAS 35  
*Candoia aspersa* +++++ 410, 650, AL 48  
*Causus defilippi* X 392, 376, DGB & EVC 75  
*Causus lineatus* + 574, 661, RFL 56  
*Causus resimus* + 574, 661, RFL 56  
*Chamaeleo adolfriederici* X 65, 63, GFW 65  
*Chamaeleo anchietae* +++ 71, 90, GFW 65  
*Chamaeleo bitaeniatus ellioti* ++ 81, 97, GFW 65  
*Chamaeleo bitaeniatus graueri* X 160, 160, GFW 41  
*Chamaeleo chapini* +++++ 44, 80, GFW 65  
*Chamaeleo dilepis idjwiensis* + 135, 150, GFW 65  
*Chamaeleo gracilis* X 163, 160, GFW 65  
*Chamaeleo ituriensis* + 102, 114, GFW 65  
*Chamaeleo johnstoni* X 128, 127, GFW 65  
*Chamaeleo oweni* X 137, 132, GFW 65  
*Chamaeleo roperi* + 110, 123, GFW 65  
*Chamaeleo rufus* X 74, 74, GFW 65  
*Chamaeleo senegalensis* ++ 102, 123, GFW 65  
*Chersina angulata* —— 264, 163, AL & EEW 57  
*Chironius carinatus* — 1359, 1196, JRD & PS 77  
*Chironius fuscus* — 1385, 1218, JRD & PS 77  
*Chrysopela ornata* + 740, 825, MAS 43  
*Cnemidophorus deppei infernalis* — 84, 75, WED & JW 60  
*Cnemidophorus guttatus flavolineatus* —— 113, 93, WED & JW 60  
*Cnemidophorus lineatissimus duodecimlineatus* —— 92, 72, WED & JW 60  
*Coleonyx brevis* X 56, 59, LMK 45  
*Coleonyx elegans* X 92, 97, LMK 45  
*Coleonyx mitratus* X 91, 88, LMK 45  
*Coluber karelini* ++ 610, 710, MAS 43  
*Coluber ravidgieri* — 875, 785, MAS 43  
*Coluber ventromaculatus* — 815, 715, MAS 43  
*Coniophanes bipunctatus* +++ 402, 560, JRB 38  
*Corallus caninus* + 908, 1040, WED 78  
*Corallus enydris* X 1643, 1700 (totals), JRD & PS 77  
*Cordylus capensis* X 100, 98, VFMF 43  
*Cordylus coeruleopunctatus* X 80, 79, VFMF 43  
*Cordylus giganteus* X 180, 176, VFMF 43  
*Cordylus jonesi* + 73, 82, UVP 66  
*Cordylus jordani* X 125, 127, VFMF 43  
*Cordylus polyzonus* + 113, 110 VFMF 43  
*Cordylus tropidosternum* X 86, 88, VFMF 43

- Cordylus vandami* + 118, 132, UVP 66  
*Cordylus warreni* ++ 110, 127, UVP 66  
*Coronella brachyura* — 440, 395, MAS 43  
*Crotaphopeltis degeneri* X 463, 447, CRSP 74  
*Ctenoblepharis nigriceps* — 89, 75, RDB 66
- Dasypeltis atra* +++ 625, 841, CRSP 74  
*Dasypeltis fasciata* ++ 645, 809, CRSP 74  
*Dasypeltis medici* ++ 600, 700  
*Dendrelaphis ahaetulla* + 735, 820, MAS 43  
*Dendrelaphis picta* ++ 725, 910, MAS 43  
*Dendroaspis angusticeps* X 1453, 1480, DGB & EVC 75  
*Dendroaspis jaimesoni* + 1650, 1901, KPS 23  
*Dendroaspis polylepis* X 2330, 2382, DGB & EVC 75; UVP 66  
*Diploglossus costatus* — 127, 116, AS 70  
*Diploglossus curtissi* — 86, 82, AS 70  
*Diploglossus occiduus* —— 305, 256, AS 70  
*Diploglossus stenurus* —— 172, 143, AS 70  
*Diploglossus warreni* — 230, 218, AS 70  
*Dipsadoboia duchesnei* —— 740, 616, RFL 56  
*Dipsadoboia elongata* —— 740, 623, RFL 56  
*Dipsas pavonina* — 544, 486, JAP 60  
*Dipsas variegata* X 640, 639, JAP 60  
*Duberria rhodesiana* +++ 220, 325 VFMF 62  
*Duberria variegata* +++ 176, 280 VFMF 62
- Elaphe helena* +++ 700, 1060, MAS 43  
*Elaphe hodgsoni* —— 1190, 995, MAS 43  
*Elaphe taeniata* ++ 1300, 1640, MAS 43  
*Elapops modestus* +++ 362, 464, KPS 23  
*Elapsoidea guentheri* X 480, 485, RFL 56  
*Elapsoidea loveridgei* + 510, 550, CRSP 74  
*Elapsoidea loveridgei colletti* + 515, 555, CRSP 74  
*Elapsoidea semiannulata* X 605, 603, DGB & EVC 75
- Emoia baudini* X 55, 55, AL 48  
*Enhydris boucouri* +++ 520, 990, MAS 43  
*Enhydris chinensis* + 516, 567, CHP 35  
*Enhydris plumbea* + 358, 378, CHP 35  
*Enyalius bilineatus* ++ 88, 105, RE 69  
*Enyalius boulengeri* + 107, 117, RE 69  
*Enyalius catenatus* X 107, 107, RE 69  
*Enyalius iheringi* ++ 100, 124, RE 64  
*Epicrates angulifer* +++ 1743, 2250, BRS & AS 74
- Epicrates fordii* —— 860, 730, BRS & AS 74  
*Epicrates gracilis* X 870, 905, BRS & AS 74  
*Epicrates striatus* — 2320, 2055, BRS & AS 74  
*Eremias argus* + 57, 61, RGW, JKJ & GWB 62  
*Eremias breviceps* — 46, 43, RM 55  
*Eremias burchelli* + 52, 57, VFMF 43  
*Eremias capensis* — 63, 58, VFMF 43  
*Eremias lineoocellata* X 57, 55, VFMF 43  
*Eremias undata* X 54, 52, VFMF 43  
*Eryx conicus* +++ 445, 855, MAS 43  
*Eryx johni* + 800, 920, MAS 43  
*Eumeces copei* + 66, 73, JRD 69  
*Eumeces dugesii* X 66, 69, JRD 69
- Garthia dorbignyi* X 40, 40, RD 66
- Garthia penai* X 32, 32, RD 66  
*Gastrophysix smaragdina* ++ 562, 682, RFL 56  
*Gecko japonicus* —— 60, 43, YO 36  
*Gecko vittatus* X 93, 95, AL 48  
*Geochelone pardalis* +++ 302, 432, RM 55  
*Geochelone pardalis babcocki* + 364, 385, RM 55  
*Gerrhosaurus flavigularis* X 126, 133, var.  
*Goniocephalus modestus* — 87, 83, AL 48  
*Gonyosoma oxycephala* + 1400, 1600, MAS 43  
*Grayia ornata* + 892, 1038, KPS 23  
*Grayia smythii* X 1321, 1321 (total), CRSP 74  
*Grayia tholloni* +++ 475, 605, CRSP 74
- Haplocercus ceylonensis* ++ 315, 380, MAS 43  
*Helicops angulatus* ++ 426, 495, JRD & PS 77  
*Hemichatus hemichatus* +++++ 635, 865, DGB & EVC 75  
*Homopus areolatus* ++ 96, 114, AL & EEW 57  
*Homopus boulengeri* X 108, 110, AL & EEW 57  
*Homopus femoralis* ++ 133, 157, AL & EEW 57  
*Hydrophis brookei* X 920, 890, MAS 43  
*Hydrophis coeruleascens* — 720, 675, MAS 43  
*Hydrophis cyanocinctus* ++ 1370, 1750, MAS 43  
*Hydrophis fasciatus* — 1010, 915, MAS 43  
*Hydrophis klossi* + 975, 1190, MAS 43  
*Hydrophis lapemoides* X 870, 855, MAS 43  
*Hydrophis mammillaris* X 730, 755, MAS 43  
*Hydrophis obscurus* + 1055, 1090, MAS 43  
*Hydrophis ornatus* — 835, 780, MAS 43  
*Hydrophis spiralis* + 1480, 1710, MAS 43  
*Hydrophis stricticollis* X 910, 960, MAS 43  
*Hypnale hypnale* +++ 275, 415, HKG 77  
*Hypnale walli* — 262, 248, HKG 77  
*Hypsilegna torquata* +++ 479, 642, WWT 44
- Ichnotropis bivittata* + 50, 54, GFW 53
- Kinixys belliana* + 193, 207, AL & EEW 57  
*Kinixys belliana nogueyi* X 152, 135, AL & EEW 57
- Kinixys erosa* —— 323, 260, AL & EEW 57  
*Kinixys homeana* X 200, 210, AL & EEW 57
- Lacerta tiliqua* — 65, 59, BL & BB 74  
*Lacerta tiliqua pardii* — 73, 64, BL & BB 74
- Lamprophis aurora* +++ 459, 529, VFMF 62  
*Lamprophis inornatus* +++ 637, 975, VFMF 62
- Laticauda colubrina* +++ 745, 1275, MAS 43
- Laticauda laticauda* ++ 800, 960, MAS 43  
*Leiocephalus barbonensis* —— 74, 60, AS 67  
*Leiocephalus barbonensis aureus* —— 79, 62, AS 67
- Leiocephalus beatus* —— 80, 64, AS 67  
*Leiocephalus beatus oxygaster* —— 80, 60, AS 67
- Leiocephalus lunatus* —— 67, 55, AS 67  
*Leiocephalus lunatus arenicolor* —— 65, 53, AS 67

- Leiocephalus lunatus melaenacelis* X 61, 60, AS 67
- Leiocephalus lunatus thomasi* —— 66, 55, AS 67
- Leiocephalus personatus* —— 79, 62, AS 67
- Leiocephalus personatus actitis* —— 86, 61, AS 67
- Leiocephalus personatus agraulus* —— 74, 60, AS 67
- Leiocephalus personatus budeni* —— 66, 52, AS 67
- Leiocephalus personatus mentalis* —— 72, 58, AS 67
- Leiocephalus personatus scalaris* —— 82, 63, AS 67
- Leiocephalus personatus tarachodes* —— 75, 63, AS 67
- Leiocephalus personatus trujilloensis* —— 78, 60, AS 67
- Leiocephalus vinculum* — 77, 73, AS 67
- Leiocephalus vinculum altavelenus* — 71, 63, AS 67
- Leiolepis belliana* — 124, 115, RM 61
- Lepidochelys olivacea* + 730, 790, AEC 52
- Leptodeira annulata ashmeadi* ++ 525, 615, WED 58
- Leptodeira annulata cussiliris* + 510, 670, WED 58
- Leptodeira annulata rhombifera* ++ 515, 630, WED 58
- Leptodeira frenata* ++ 464, 576, WED 58
- Leptodeira nigrofasciata* + 430, 473, WED 58
- Leptodeira polysticta* ++ 520, 700, WED 58
- Leptodeira punctata* + 410, 445, WED 58
- Leptodeira septentrionalis* + 595, 774, WED 58
- Leptodeira septentrionalis ornata* + 500, 665, WED 58
- Liolaemus constanzae* — 61.5, 54, RD 66
- Liolaemus fuscus* — 50, 46, RD 66
- Liolaemus lemniscatus* — 52.4, 49.5, RD 66
- Liolaemus magellanicus* X 60, 62, RD 66
- Liolaemus monticola* X 61, 63, RD 66
- Liolaemus nigroviridis* — 74, 64, RD 66
- Liolaemus pictus* X 64, 62, RD 66
- Liolaemus platei* — 53, 44, RD 66
- Liolaemus tenuis* X 54, 55, RD 66
- Liopeltis calamaria* + 227, 290, MAS 43
- Liopeltis frenatus* — 525, 450, MAS 43
- Liopeltis rappi* X 340, 330, MAS 43
- Liopeltis scriptus* X 310, 320, MAS 43
- Liopeltis stoliczkae* — 375, 343, MAS 43
- Lycodon aulicus* + 692, 737, CHP 35
- Lycodon jara* + 420, 445, MAS 43
- Lycodon subcinctus* + 710, 820, MAS 43
- Lycodon travancoricus* + 475, 505, MAS 43
- Lycodonomorphus laevissimus* + 725, 915, VFMF 62
- Lycodonomorphus leleupi* + 580, 750, DGB & EVC 75
- Lycodonomorphus rufulus* + 552, 702, VFMF 62
- Lycophidion laterale* X 391, 409, KPS 23
- Lycophidion ornatum* + + + 321, 416, CRSP 74
- Lycophidion semiannule* X 222, 228, VFMF 62
- Lycophidion variegatum* + 320, 340, DGB & EVC 75
- Lygodactylus angolensis* X 31, 32, GFW 53
- Lygodactylus angularis* — 39, 35, GFW 53
- Lygodactylus capensis* X 31, 31, AEL 53
- Lygodactylus picturatus* — 41, 36, GFW 53
- Lygosoma graueri* + 172, 192, GFW 41 (total lengths)
- Lygosoma kilimense* + 54, 59, GFW 53
- Lygosoma luberoensis* — 138, 131 GFW 41 (total lengths)
- Lygosoma solomonis* — 67, 63, AL 48
- Lytorhynchus diadema* — 429, 391, AEL & SCA 70
- Mabuya capense* X 130, 135, VFMF 43
- Mabuya lacertiformis* + 48, 52, AL 53
- Mabuya megalura* + + + 56, 73, GFW 53
- Mabuya perroteti* — 133, 124, GFW 53
- Mabuya quinquetaeniata* + + 121, 151, GFW 53
- Mabuya quinquetaeniata obsti* X 117, 114, AL 53
- Mabuya rudis* X 76, 77, RM 59
- Mabuya striata chimbawa* + 77, 82, AL 53
- Mabuya striata ellenbergi* X 93, 90, AL 53
- Mabuya sulcata* + 75.5, 81, VFMF 43
- Macropisthodon plumbeicolor* + + + + 415, 605, MAS 43
- Malacoctenus tornieri* + + 145, 177, AL & EEW 57
- Mehelya capensis* + + 1220, 1500, DGB & EVC 75
- Mehelya poensis* + + + + 642, 936, KPS 23
- Mehelya savorgnani* + + 884, 1021, RFL 56
- Mehelya stenophthalmus* + + + + 455, 585, RFL 56
- Meizodon coronatus* + 478, 517, CRSP 74
- Meizodon semiornatus* + + + 455, 600, CRSP 74
- Micrelaps boettgeri* + + + + 264, 381, CRSP 74
- Micrurus allenii* + + 800, 951, JMS & JLV 74
- Micrurus langsdorffi* + 685, 761, JRD & PS 77
- Micrurus nigrocinctus* + + + 575, 760, JMS & JLV 74
- Micrurus spixii* — — — 1315, 820, JRD & PS 77
- Microcephalus cantoris* —— 1410, 1155, MAS 43
- Microcephalus gracilis* + 870, 930, MAS 43
- Miodon christyi* + + + 690, 795, GW & RL 47
- Miodon collaris* + + + 501, 630, CRSP 74
- Miodon collaris graueri* + 310, 358, CRSP 74
- Naja haje* — 2125, 1946, DGB & EVC 75
- Naja mossambica* X 1285, 1270, DGB & EVC 75
- Naja naja samarensis* + 843, 921, AEL 64
- Nerodia fasciata clarki* + + + + AHW & AAW 57
- Neusticurus cochranae* + 70, 79, TMU 66
- Neusticurus rufus* X 88, 89, TMU 66

- Neusticurus strangulatus* — 87, 76, TMU 66  
*Neusticurus tatei* — 104, 93, TMU 66  
*Nucras delalandii* X 99, 99, VFMF 43  
*Nucras tessellata* — 84, 76, VFMF 43
- Oligodon barroni* + 280, 310, MAS 43  
*Oligodon catenata* X 490, 473, MAS 43  
*Oligodon cinereus* + 620, 695, MAS 43  
*Oligodon cruentatus* ++ 300, 320, MAS 43  
*Oligodon cyclurus* — 800, 630, MAS 43  
*Oligodon melaneus* — 275, 255, MAS 43  
*Oligodon splendidus* X 610, 630, MAS 43  
*Oligodon taeniatus* + 387, 427, MAS 43  
*Oligodon taeniolatus* X 280, 285, MAS 43  
*Opheodrys multicinctus* — 755, 640, MAS 43  
*Opipreuter xestus* + 51, 58, TMU 69  
*Opisthotropis latouchii* + 395, 419, CHP 35  
*Oxybelis argenteus* X 714, 743, JRD & PS 77  
*Oxyrhabdium modestum* ++ 449, 521, MAS 43  
*Oxyrhopus trigeminus* + 579, 888, JRD & PS 77
- Pachydactylus punctatus* + 38, 42, GFW 53  
*Pachydactylus tuberculatus* — 72, 67, GFW 53  
*Palmatogecko rangei* ++ 60, 68, VFMF 43  
*Pareas margaritiphorus* + 270, 395, MAS 43  
*Pareas monticola* + 430, 500, MAS 43  
*Phelsuma laticauda* — 52, 42, RM 64  
*Phelsuma lineata* — 57, 47, RM 64  
*Phelsuma madagascarensis* — 95, 83, RM 62  
*Philothamnus heterodermus* + 515, 730, CRSP 74  
*Philothamnus heterolepidotus* + 475, 527  
*Philothamnus natalensis* ++ 855, 1062, UVP 66  
*Philothamnus ornatus* + 420, 515, DGB & EVC 75
- Pholidobolus affinis* — 64, 58, RRM 73  
*Pholidobolus macbrydei* X 56, 56, RRM 73  
*Pholidobolus montium* ++ 56, 66, RRM 73  
*Pholidobolus prefrontalis* + 57, 63, RRM 73  
*Phrynocephalus ornatus* X 39.5, 41.5, AEL 59  
*Phyllorhynchus browni* — 783, 692, AWH & AAW 57
- Physignathus concinnus* — 250, 200, MAS 35  
*Platysaurus capensis* X 78, 75, VFMF 43  
*Platysaurus guttatus* — 88, 84, VFMF 43  
*Platysaurus intermedius* — 88, 84, UVP 66  
*Platysaurus mitchelli* X 46, 48, VFMF 43  
*Praescutata viperina* — 825, 740, MAS 43  
*Prosymna bivittata* + 275, 387, UVP 66  
*Prosymna jani* ++ 182, 223, VFMF 62  
*Prosymna lineata* — 262, 229, VFMF 62  
*Prosymna sundevalli* + 247, 362, DGB & EVC 75
- Psammobates oculifer* + 118, 133, AL & EEW 57  
*Psammobates tentorioides* + 100, 138, AL & EEW 57  
*Psammobates tentorioides verroxi* + 118, 141, AL & EEW 57
- Psammophis angolensis* + 320, 350, DGB & EVC 75
- Psammophis crucifer* X 490, 490, DGB & EVC 75  
*Psammophis jallae* — 762, 640, DGB & EVC 75  
*Psammophis punctulatus* — 1080, 972, CRSP 74  
*Psammophis subtaeniatus* — 900, 820, DGB & EVC 75
- Pseudaspis cana* X 1105, 1140, DGB & EVC 75  
*Pseudemys floridana texana* + 244, 273, AEC 52
- Pseudocordylus microlepidotus* X 134, 136, VFMF 43
- Pseudocordylus wilhelmi* — 82, 69, UVP 66
- Pseudoxenodon macrops* — 930, 820, MAS 43
- Pseudoxenodon nothus* — 736, 645, CHP 35
- Pseustes poecilonotus* + 1107, 1205, JRD & PS 77
- Python sebae* + 2300, 3685, DGB & EVC 75
- Rhabdophis auriculata* + 352, 372, AEL 70  
*Rhabdophis auriculata myersi* X 342, 348, AEL 70
- Rhabdophis himalayana* + 605, 945, AEL 70
- Rhabdophis nigrocincta* X 625, 655, AEL 70
- Rhabdophis nuchalis* + 520, 740, AEL 70
- Rhabdops bicolor* + 475, 530, MAS 43
- Rhadinea brevirostris* — 372, 333, CWM 74
- Rhadinea calligaster* + 313, 401, CWM 74
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